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The ecology of the leopard Panthera pardus in the Cederberg Mountains

The ecology of the leopard *Panthera pardus* in the Cederberg Mountains

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ABSTRACT

Large predators fulfil key roles in maintaining ecosystems through controlling herbivores as well as meso-predators, all of which could impact on the natural biodiversity of an area. The greatest threat to predators and their survival is the loss of habitat and persecution by farmers due to depredation of livestock. Leopards in the Western Cape, South Africa, have managed to survive intense persecution and severe perturbation of their habitat, and are now the last remaining large predator in the area, inhabiting rugged and inhospitable mountains. Whilst leopards have been studied in detail in different habitats of Africa, including forests and savanna, there is a paucity of ecological information from the isolated population of comparatively small leopards found in the Cederberg Mountains of the Western Cape. Between 2004 and 2010, these leopards were studied using remote infra-red camera traps and GPS radio-collars to record data on their home ranges, population density, movements, activity, diet and future status in a human impacted habitat with no large competing carnivores. Working in two biomes, GPS location data were obtained from 11 radio-collared leopards (7 males, 4 females). Homes range sizes were up to 910 km^2 (95% MCP) for leopards in the Karoo biome, some of the largest recorded for the species. Male ranges were significantly larger than female ranges, and daily displacement for leopards was as much as 30 km. 193 camera trap photographs of 7 adult leopards (2 males, 5 females) were obtained in the Karoo between 2004 and 2007. Combining camera trap and radio-collar data, leopard densities were estimated as 0.25 – 0.99 leopards/100 km^2 in the Karoo and 1.8 – 2.3 leopards/100 km^2 in the Fynbos biome. Leopards were largely nocturnal despite having no large competing predators. Their movements did not appear to be influenced by human activity. Their primary food items were klipspringers and rock hyrax, diurnal herbivores that constituted 78% of their diet. Livestock were an insignificant prey item. The mountain Fynbos remains largely unchanged. Conservation of this area, carefully managing leopard-conflict situations and identifying possible corridors to aid leopard dispersal, should ensure the long-term conservation of the species here. However, recent transformation of the Karoo suggests further steps need to be investigated, including the possibility of reintroducing an extinct guild of large carnivores, to re-establish a fully functioning system over a greater area.

ACKNOWLEDGEMENTS

My love and passion for wild places began thirty-three years ago when my father would take my brother and me fishing. Watching otters glide through the steel-grey water on a winter's morning with the call of fish eagles in the background were the images that set me on my course and have stayed with me my whole life. Returning to our old haunts as a young adult, I saw no otters, no eagles and signs of serious habitat degradation and pollution. This project has been a way for me to give something back to our beautiful planet.

I must thank my mom for planting the seed that I would someday be a scientist, and for all her unconditional love, care and unlimited supply of the one essential ingredient for living in the mountains - rusks.

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Author's declaration

I declare that the work in this dissertation was carried out in accordance with the regulations of the University of Bristol. I had help from Willem Titus for leopard captures and Therèsè Rautenbach conducted the scat analyses. With those exceptions, I declare that the work in this thesis is my own, none of which has been submitted for any other academic award. The views expressed in the thesis are those of the author.

Quinton Martins

October 2010

Dedication

This thesis is dedicated to my late father, my mom, and my loving wife, Elizabeth Joy Martins

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CHAPTER 1

Introduction

1.1. Top predators and their role in the ecosystem

Extinctions on our planet have been a part of nature's process since the first signs of life. Today conservationists are extremely concerned about the recent upsurge in the number of extinctions and the effect these may have on ecological systems. Humans have had an unprecedented effect on their ecosystem. Over the last 50,000 years we have witnessed the loss of a considerable proportion of the megafauna across the globe (Terborgh & Estes, 2010). It is possible that climate change, and as a result, changes in vegetation, has contributed to extinctions (Allen *et al.*, 2010). Nevertheless, as humans became industrialized, colonization and destruction of the earth's natural resources escalated. Over the past 500 years, human activities have led to at least a quarter of the world's known mammal extinctions or those threatened with extinction (Schippers, 2008). The elimination of the world's megafauna included the loss of most of the large predators.

It has not helped that biologists have contributed to the demise of large predators. In some instances, predators were purposefully killed to minimise their supposed negative impact on the system (Cobb, 1981). Notwithstanding, conservation biologists supporting 'bottom-up' control processes would not necessarily be perturbed at the decline in large predator numbers, because they occur last on the food chain. The argument was that where a system is regulated from the bottom up, predators are last in this chain and so would contribute very little to the system (Estes & Holt, 2001; Miller *et al.*, 2001). These well-orchestrated arguments suggested that the removal of top trophic levels result in lower trophic levels remaining intact, whereas the removal of lower primary producer levels would cause far greater disruption to the ecosystem (Hunter & Price, 1992). Conversely, Elton (1927) and Hairston *et al.* (1960) promoted the idea that because 'the world is green' it is obviously not overgrazed by herbivores. Therefore, if it is not the food that limits the herbivores, it must be the predators (Miller *et al.*, 2001; Terborgh *et al.*, 2001). These are often keystone species, regulating the number of herbivores in the trophic level below them, thereby reducing their impact on the plant communities, the lowest basic trophic level. This

was regarded as a 'top-down' control process. Over the past 50 years, considerable work has been done to illustrate the importance of large predators in an ecosystem, and how they have a significant impact on the structuring and functioning of healthy ecosystems (Terborgh & Estes, 2010). Despite arguments in favour of one process or the other, the overall consensus is that a combination of both bottom-up and top-down processes occur concurrently (Seidensticker, 2002).

The fine balance needed for a healthy ecosystem is built around dynamism, where interactions are in a constant state of flux (Terborgh & Estes, 2010). Certain components of the system may play bigger roles than others. However, major disturbances or imbalances can result in what Paine (1980) described as a 'trophic cascade'. Terborgh *et al.* (2001) observed the chain reactions resulting from the sudden formation of small islands of habitat caused by anthropogenic factors in Venezuela. The islands were too small for large predators such as jaguars *Panthera onca*, resulting in an increase in the number of herbivore species, which subsequently destroyed the vegetation (Terborgh *et al.*, 2001). Similarly, the opposite effects are seen in case studies when keystone predators such as wolves *Canis lupus* or bears *Ursus* spp. have been reintroduced into ecosystems where their absence had led to overpopulation of prey species (Ripple & Beschta, 2004, 2008; Beschta & Ripple, 2009).

The effects of these reintroductions demonstrate the importance of predators and that the extirpation or local decline of large carnivores perturbs the biological communities in which they live. The extent of these declining predator populations may alter entire ecosystems (Schaller, 1972; Henke & Bryant, 1999; Miller *et al.*, 2001; Terborgh *et al.*, 2001; Treves & Karanth, 2002; Seidensticker, 2002; Wilting *et al.*, 2006). Thus, the conservation of large carnivores is of global importance as they serve as umbrella species across habitats, ensuring broader conservation of the ecosystems in which they live (Noss *et al.*, 1996).

Left unchecked, loss of top predators can, for instance, result in meso-predator release, whereby population densities of these smaller predators may increase to a point where they have a negative impact on smaller prey. In such cases, top predators form the 'watch-dogs', maintaining a balance through interspecific killing of other predators (Palomares & Caro, 1999).

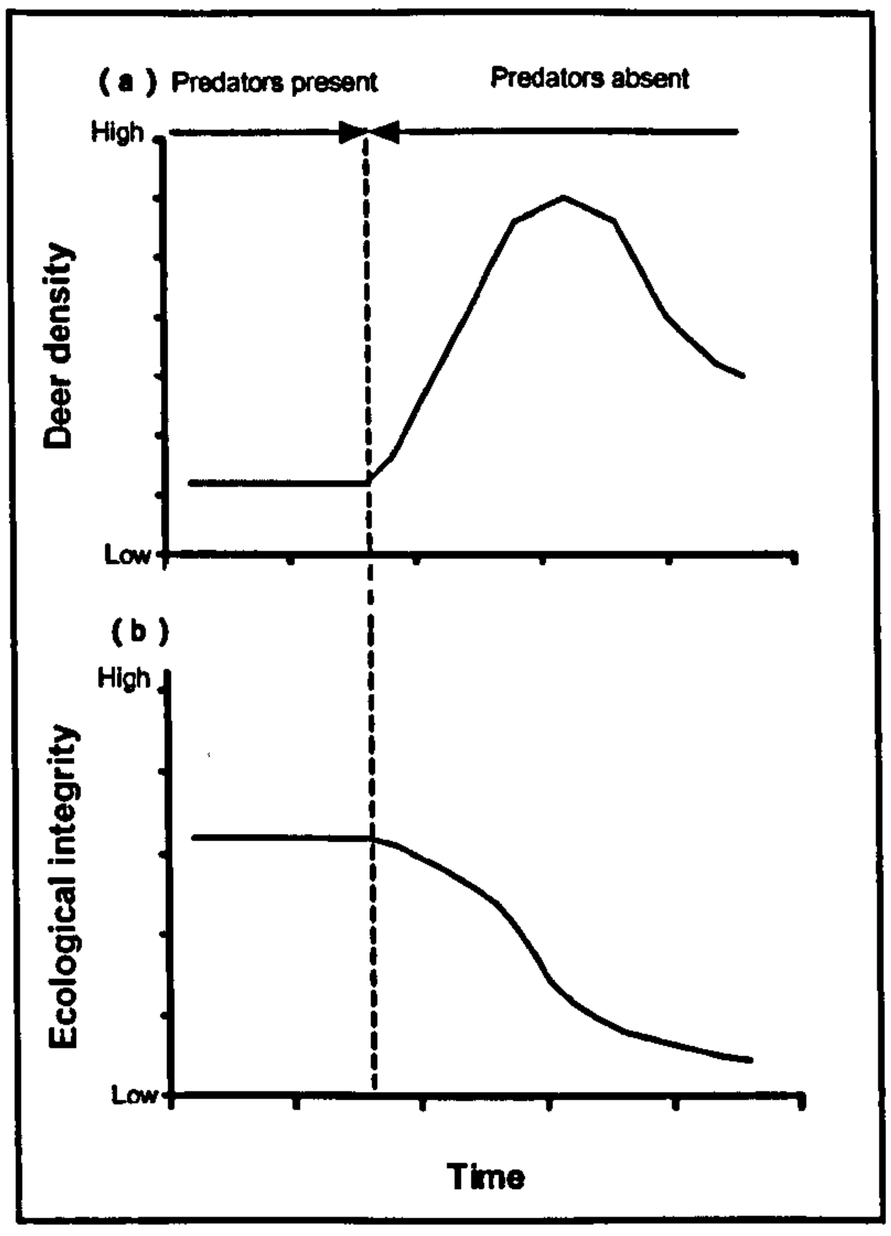


Figure 1.1. Figure showing numerical response of deer after removal of large predators (a) and the consequent loss of ecological integrity with increased browsing pressure (b). From Ripple *et al.* (2010).

Where ecosystems are lacking integral components, such as large herbivores and/or large carnivores, regaining the functionality of that system may require the reintroduction of species. In many cases, megafauna indigenous to these ecosystems are extinct, and have been for thousands of years (Donlan *et al.*, 2005). Efforts to restore large wild vertebrates where the original species no longer exist are termed 'rewilding' (Donlan *et al.*, 2005). In the hope of restoring ecosystem integrity, protagonists are attempting refaunation based on events dating back to the Pleistocene. Griffith & Harris (2010) suggest that it is unlikely the trophic cascades that followed the megafaunal extinctions of the Pleistocene can still be a concern today. Therefore, undoing perturbations observed in an ecosystem should focus on reversing more recent changes. Despite arguments against the use of exotic or proxy species to fill the role of extinct species (Oliveira-Santos & Fernadez, 2010), this luxury is not always available and alternate, suitable species may be used without threats of disease, invasiveness or damage to the existing ecosystem (Griffith & Harris, 2010). Caution is required when introducing new species, indigenous or not, and care should be taken to exercise vigilance in monitoring the effects so as to terminate the experiment should there be adverse impacts.

1.2. Predators in Africa

It is clearly important to have large predators to ensure that functioning ecosystems are sustained. Where these have been lost, re-establishing populations would appear to be the logical solution, and this has worked in many instances (Ripple & Beschta, 2004, 2008). Africa has perhaps had the fewest extinctions and an intact assemblage of megafauna generally still exists (Hayward, 2009). Following suggestions made by Oliveira-Santos & Fernadez (2010), where local extinctions have occurred, it would be possible to ensure refaunation through reintroduction of extant species. However, other than in large conserved areas, the reintroduction of large predators is potentially a problem. Large predators need sufficiently large habitat with a suitable prey base in which to support viable populations; these usually only exist in large conserved areas or reserves (Noss *et al.*, 1996). The co-existence of modern humans with large predators outside conserved areas has been hampered by the total destruction or altering of habitats, threat of personal safety and the impact on livestock production. It is perhaps not surprising that, in many cases, the edges of conserved areas are high conflict zones (Woodroffe & Ginsberg, 1998).

Africa was one of the last refuges for the world's megafauna and large predators. Humans and their ancestors have co-existed with large predators for 4 million years (Treves & Naughton-Treves, 1999). In the last century, we have seen a substantial range loss for large mammals, with the real threat of extinction for many species. This coincides with an escalation of the human population in Africa, increasing the likelihood of conflict with wildlife, exerting more pressure on the already threatened carnivore populations (Hayward, 2009).

Understanding how ecosystems function is key to their conservation. Broader perspectives are often neglected in research due to the daunting spatial scales involved and their lack of amenability to study (Seidensticker, 2002). The difficulties that arise in the conservation of keystone species are exacerbated by their elusive nature, particularly large predators. Furthermore, difficulties arise in their complex interactions with humans (Woodroffe & Ginsberg, 1998). The long-term persistence of 'source' populations may depend on their densities within protected areas. However, persecution in marginal areas or land surrounding these core protected areas, and the resulting edge effects, may result in these populations becoming 'sinks' or even experiencing local extinctions (Seidensticker,

2002). As a result, the effective conservation of top carnivores seems to depend largely on the protective measures that can be implemented outside existing conservation areas (Woodroffe & Ginsberg, 1998; Balme *et al.*, 2010).

Twenty-six percent of mammals in the Order Carnivora face extinction or have been extirpated (Schipper *et al.*, 2008). Loss of habitat in combination with direct persecution are the primary factors affecting the survival of large predators (Norton, 1986; Weber & Rabinowitz, 1996; Woodroffe & Ginsberg, 1998). Other factors such as hunting, disease, climate change and loss of biological fitness can also impact on predator populations, especially those that have undergone significant population reductions.

The combination of so many interacting factors presents a significant conservation challenge. The availability of suitable habitat is becoming more of a problem with human encroachment and the resulting habitat fragmentation, compounded by the small populations or low densities at which large carnivores naturally exist, making them even more vulnerable to extinction. A lot more data are needed to find solutions to these problems and unravel the current quandary.

1.3. Leopard *Panthera pardus* (Linnaeus, 1758)

Leopards face many of the same threats as other large predators, though they are one of the most widely distributed and, to a large extent, resilient of the larger carnivores (Fig. 1.2). Remarkably, leopards are still present throughout the majority of their historical range and in some areas appear even to be able to co-exist with humans, albeit with consequences such as loss of human life and depredation of livestock, as in parts of India (Athreya, 2006). However, generally it appears that leopard populations are declining over the majority of their range outside large protected areas, with local population extinctions increasing.

Leopards are solitary cats and the most secretive of the large carnivores. Although predominantly nocturnal (Hamilton, 1976; Bailey, 1993; Stander, 1998), they are also active and hunt during the day (Bailey, 1993; Kure, 2003). Yet comparatively little is known about their behaviour due to the difficulty in observing them. Research on leopards in Africa has mainly taken place in the savanna and forest areas. Extant populations occurring in large protected areas, such as the Kruger National Park (*c.* 21,000 km^2), have stable leopard populations (Le

Figure 1.2. Distribution of leopards in Africa (taken from http://www.iucnredlist.org/apps/redlist/details/15954/0/rangemap; accessed 22/10/2010)

Roux & Skinner, 1989; Bailey, 1993). However, their movement is not limited to fenced reserves, creating threatened sub-populations. The population within the Western Cape, South Africa, is one such population, and typifies the increasing number of small and relatively isolated leopard populations (Fig. 1.3). We know even less about the ecology of fragmented leopard populations such as the one inhabiting the mountains of the Western Cape.

Reliable population estimates of large carnivores and an understanding of their ecology are essential for effective conservation management (Stander, 1998). Martin & de Meulenaer's (1988) estimate of 714,000 leopards in sub-Saharan Africa, with 23,472 in South Africa, has been criticized by Norton (1990) as an "over-estimate" that may have negatively affected leopard populations by fostering complacency among the authorities charged with their management. Although the negative impacts on large contiguous leopard populations in optimum habitat are probably negligible, the same cannot be said of small, persecuted and isolated populations.

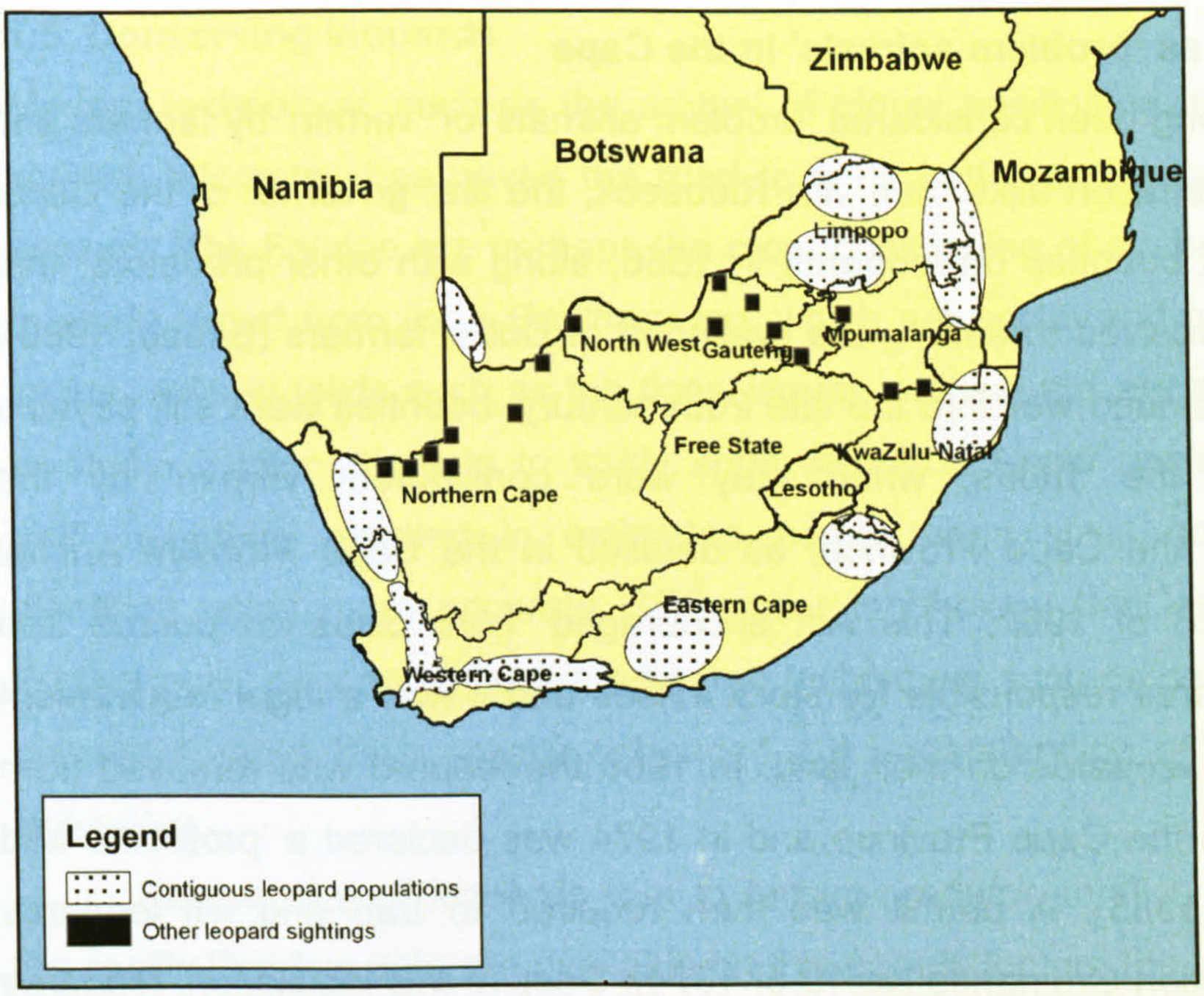


Figure 1.3. Distribution of leopards in South Africa. Data taken from Daily *et al.* (2005) for all provinces except for the Western and Northern Cape, where data from Q. Martins (unpubl. data).

1.4. Leopards of the Cape

1.4.1. Historical status of leopards in the area

The first written records of leopards in southern Africa were from the Cape over 400 years ago (Shortridge, 1934; Skead, 1980). Historical evidence suggests that leopards were heavily persecuted and finally disappeared from the Cape Peninsula in the mid- to late 1800s and can now only be found in the surrounding mountain regions (Skead, 1980; Norton & Lawson, 1985; Norton, 1986). Despite extensive habitat loss and reduction in prey numbers and distribution, leopards have managed to persist in these mountains, and now fill the role of the apex predator in the Western Cape ecosystem. Here they occur within a continuous mountain chain also known as the Cape Folded Belt. The effect of human habitation has resulted in fragmentation of this habitat, with core protected areas being surrounded by marginal inhabited areas. Furthermore, despite leopards being such adaptable cats, in the Cape they appear to avoid certain habitats, such as big open areas (Schaller, 1972). This, like tigers *Panthera tigris* (Seidensticker, 1976), may affect their dispersal capabilities, enhancing their risk of local extinction.

1.4.2. Leopards as 'problem animals' in the Cape

Leopards have long been considered 'problem animals' or 'vermin' by farmers and provincial administration alike. Jan van Riebeeck, the first governor of the Cape, declared the first bounties on leopards in 1656, along with other predators, that posed real or perceived threats to the livelihood of Dutch farmers (Skead, 1980). This practice continued well into the late 20th century: bounties were still payable on leopards in the 1960s, when they were considered 'vermin' by the Administration of the Cape Province, as detailed in the Cape Problem Animal Ordinance No. 26 of 1957. This Act encouraged 'hunt clubs' to pursue and exterminate leopards responsible for stock losses and it was a legal requirement for farmers to kill leopards on their land. In 1968 the leopard was removed from the 'vermin' list in the Cape Province and in 1974 was declared a 'protected wild animal' (Norton, 1986). A permit was then required to trap and kill leopards (Nature Conservation Ordinance No.19 of 1974). Despite this legislation, leopards continue to be killed in the Western Cape, without a single conviction of illegal practice. However, after the 1974 Act was passed, action was taken to minimize the number of leopards killed and research was undertaken into the ecology of the species (Norton & Lawson, 1985; Norton, 1986).

Although leopards were made protected animals, the existing legislation still allows caracals *Caracal caracal* and black-backed jackals *Canis mesomelas* to be trapped without a permit. This causes a major conservation problem for leopards, since the techniques used to kill these so-called 'problem animals', such as leg-hold traps or 'gin traps', poisons or cages, can be indiscriminate, and so there is a high risk of trapping leopards. Furthermore, until about two years ago, permits issued by the authorities for the removal of a 'problem leopard' would specify that cage traps or 'gin traps' could remain set for up to 1 month. There was then a high probability that the animal caught was not the one causing stock losses. Additionally, the injuries to non-target species caused by 'gin traps' often resulted in their death. Present legislation does not condone the use of 'gin traps' for catching leopards, but there is no specific legislation that outlaws their use for other species.

1.5. Conserving leopards

Modern technology, such as the advent of global positioning system (GPS) and satellite telemetry, has paved the road to a far better understanding of predator ecology. The Felidae are perhaps the most challenging of all the large carnivores to study. Apart from lions *Panthera leo*, which are social and generally easier to locate, solitary felids such as the tiger, jaguar and leopard are particularly difficult to study. Earlier attempts to study snow leopards *Uncia uncia* using traditional VHF telemetry resulted in estimated home range sizes one-tenth of those identified using more accurate GPS collar technology (McCarthy *et al.*, 2005). Furthermore, new non-invasive research techniques such as genetics and remote camera surveys have greatly enhanced our understanding of their ecology and behaviour.

Persecution of leopards due to farmer-predator conflict, low densities and the reality that few data are available on this population are the basis for this broad ecological study in the Cederberg Mountains of the Western Cape.

1.6 The Cederberg Mountains

Historically, the Cederberg had the highest leopard-farmer conflict in the Cape Province due to depredation of livestock (Norton & Henley, 1987). Conflict with predators may have included brown hyaenas *Parahyaena brunnea*. Leopards and hyaenas were captured in stone traps baited with an animal carcass or live bait, and killed. The last known reference to brown hyaenas in an area close to the Cederberg was by Delagorgue in 1847 (Shortridge, 1934). Although farmer-leopard conflict still occurs in the Cederberg, the influence of the leopard research and the establishment of the Cape Leopard Trust, a predator conservation organisation and registered non-profit organisation (www.capeleopard.org.za) resulted in a significant decrease in leopard mortalities in and around the study area. These influences were evident, for example, when the Cederberg Conservancy, an area of 1710 km^2 in the Cederberg, was set aside by landowners as a leopard conservation area in 2007.

The Cederberg was an ideal study site based on: (i) the presence of two of the key biomes found in the Western Cape; (ii) the existence of both conserved and perturbed habitats; (iii) a general lack of information on the species and its impact on its environment; and (iv) the need to understand the role leopards as the

apex predator have in the Cederberg, and what was required to ensure their survival.

1.7. Aims

I aimed to provide a comprehensive and robust scientific study of the ecology of leopards in the Cederberg Mountains with a particular view on their long-term conservation and alleviation of conflict with farmers. The paucity of ecological and behavioural information on the species encouraged me to determine (i) the spatial and habitat requirements of leopards in two biomes; (ii) the population densities in different biomes while assessing the most suitable methods to obtain these results; (iii) how, why and when leopards move in a rugged mountain landscape, drawing inferences from ancillary components in their environment such as prey behaviour; (iv) the prey preferences of leopards in the Cederberg, both using innovative means as well as highlighting results to mitigate human-leopard conflict; and (v) use these data to assess the future of leopards as the apex predator in the Cederberg.

1.8. Thesis structure

- In Chapter 2 I describe my study area including the climate, geology, fauna and flora in the Cederberg;
- In Chapter 3 I describe my research methods;
- In Chapter 4 I use GPS tracking to quantify the patterns of home range and habitat use by leopards in the Cederberg, and show that leopards have a preference for rocky habitat, avoid open areas and have some of the largest home ranges recorded for the species;
- In Chapter 5 I combine GPS data and the results of a camera trapping study in the Karoo to estimate leopard abundance and densities, showing that leopard densities are low. Within the Cederberg, leopards have lower densities in the Karoo biome (<1 leopard/100 km^2) than in the Fynbos (1 – 2 leopards/100 km^2);
- In Chapter 6 I look at the movements, activity and hunting behaviour of the leopards in the Cederberg and show using camera trap and GPS collar data that leopards are predominantly nocturnal, and that males move in a

more linear fashion than females. I also showed that the lack of competing large predators as well as human habitation had no significant influence on their movement. Leopards mainly hunted diurnal prey during the night.

- In Chapter 7 I use GPS cluster locations and scat analyses to quantify the diet of leopards in the Cederberg. Leopards were mainly eating klipspringers and rock hyraxes. I also show that, in this habitat, similar results are obtained using scat analyses and identifying prey remains found where I recorded clusters of GPS locations; and
- Finally, in Chapter 8, I use these data to discuss potential long-term management strategies for the leopards in the Cederberg and how best to minimise further perturbations to the ecosystem.

CHAPTER 2

Study area

2.1. Location and background to the study area

The study was carried out in the Cederberg Mountains, Western Cape, South Africa (32°27' S; 19°25' E) *c.* 200 km north of Cape Town (Fig. 2.1). The *c.* 3000 km^2 study area was delineated by drawing a polygon around the outer perimeter of all GPS collared leopards in this study, which formed part of a population extending throughout the Cape folded mountains (Norton *et al.*, 1986). The closest towns, Clanwilliam, Citrusdal and Ceres, were 80 - 120 km from my research base, Matjiesrivier Nature Reserve. Vehicular access to my base was on gravel road of 60 km. In winter, flooded roads prevented movement in or out of the reserve for up to 4 days at a time. The road from Ceres in the south was built along a fault line running north through the centre of the Cederberg, along the division between the two prominent biomes, the Karoo to the east and Fynbos to west of the road.

The Cederberg, named after the Clanwilliam Cedar tree, now Clanwilliam cypress *Widdringtonia cedarbergensis*, is a mountain area with evidence of human habitation dating back to *c.* 6000 years ago, where *San* 'bushmen' existed as hunter-gatherers, leaving behind rock art and stone tools as signs of their presence (Deacon, 1998). Approximately 4000 years later, *Khoi* pastoralists were thought to have moved into this area, sharing it with the *San.* With them, they brought the first domesticated livestock, fat-tailed sheep *Ovis aries.* Rock art from this time depicts signs of a faunal assemblage with larger mammals such as elephant *Loxodonta africana*, black rhinoceros *Diceros bicornis* and eland *Taurotragus oryx*, all species known to have inhabited the Cederberg (Cowling & Richardson, 1995). Paintings of predators such as leopard were seldom seen (Fig. 2.2).

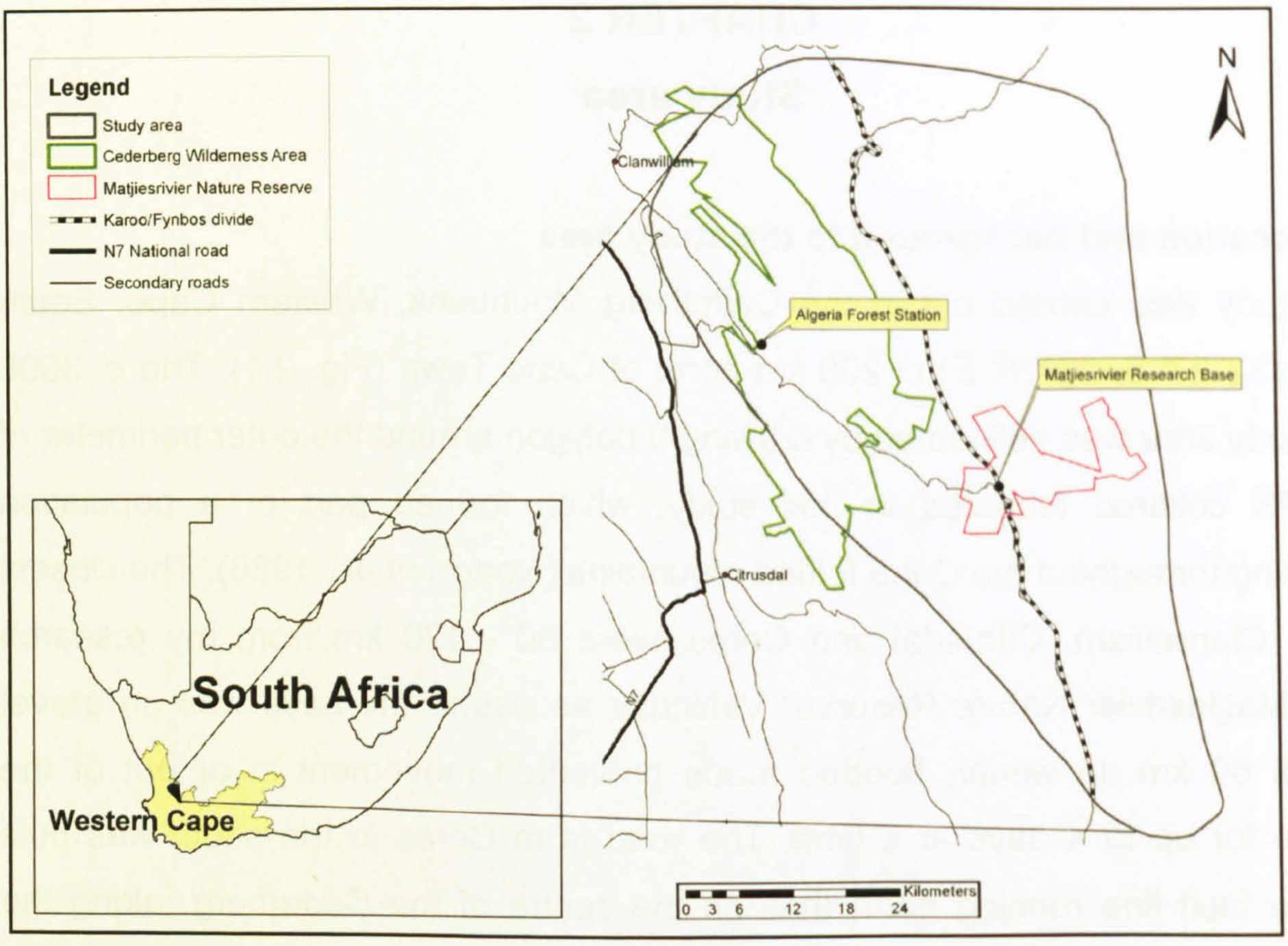


Figure 2.1. Map of the study area showing location, major towns, Cederberg Wilderness Area, Matjiesrivier Nature Reserve and the dividing line between the Karoo biome east of the line, and Fynbos biome west of the broken line.

In the Cederberg, livestock farming with sheep, goats and cattle was the predominant land use until the 1990s. By 2004, livestock farming was reduced, and wine production, olive and citrus farming in the valleys became the dominant agricultural activities. At the same time tourism became an increasingly important

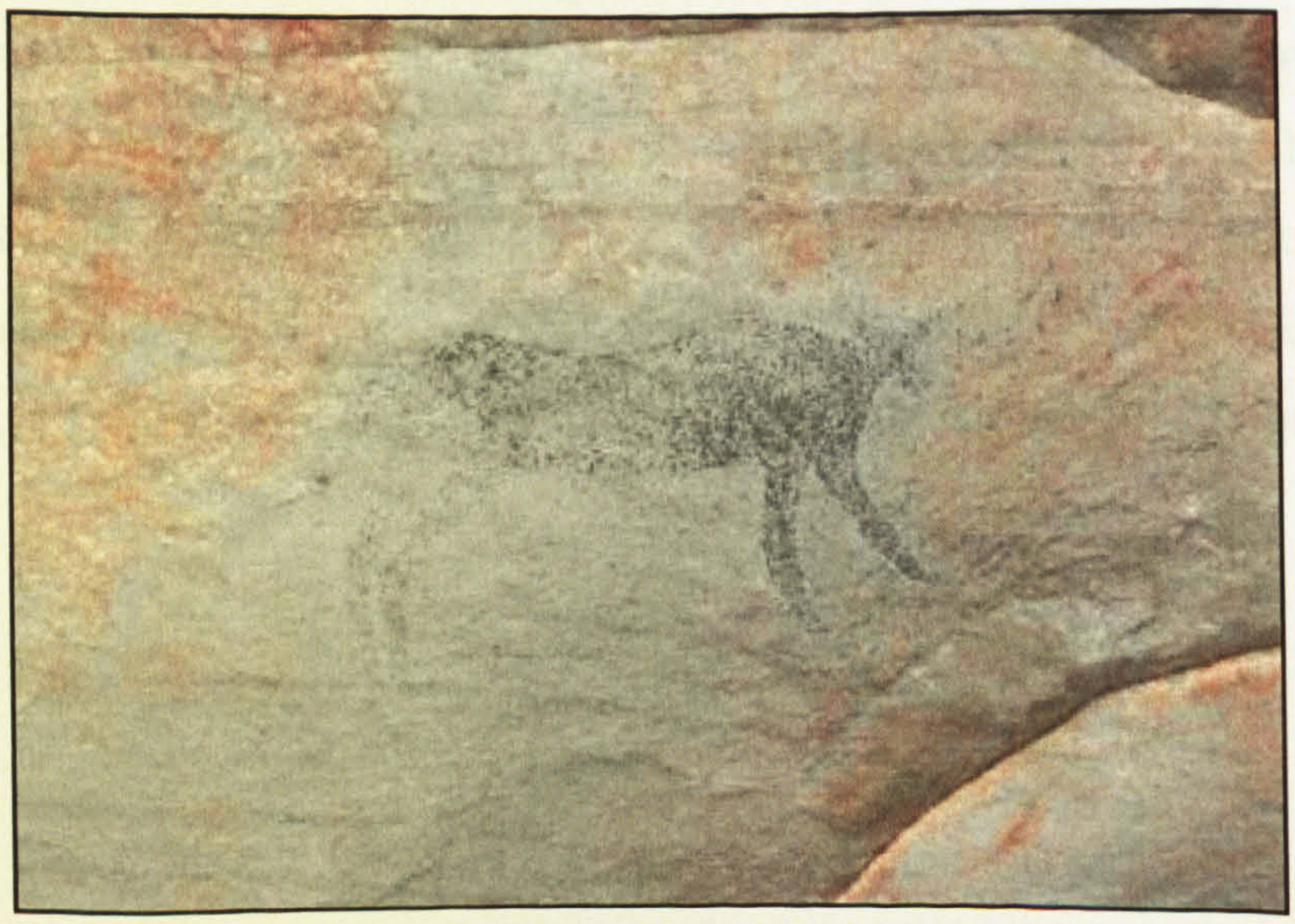


Figure 2.2. One of the few *San* rock art paintings of a leopard in the Cederberg Mountains. Paintings date back as far as 6000 years ago. Photo: Nic Wiltshire

source of local income; activities included hiking, mountain biking and horse-riding. There is a well-defined network of hiking trails in the Fynbos part of the Cederberg. These occur predominantly in the Cederberg Wilderness Area (CWA), a conservation area managed from the Algeria Forest Station by Cape Nature (CN), the statutory conservation body in the Western Cape. There were no hiking trails in the Karoo, apart from one or two footpaths used by livestock and a few people. Matjiesrivier Nature Reserve is managed by CN as part of the CWA. The creation of private nature or game reserves with reintroduced game species also added to the tourism opportunities in the Cederberg.

2.2. Climate

The austral summer extends from September to March and winter from April to August (Norton *et al.*, 1986). There was insufficient climatic variation to identify other seasons. Temperatures recorded from 2004 - 2009 at the Clanwilliam weather station ranged from 1°C at night in winter to 46°C on summer days, while average temperatures in winter were 23.6±1.5°C and 32.8±1.1°C in summer (Clanwilliam station 0084671O, -32.18S, 18.88E, elevation 102 m) (Fig. 2.3). Temperatures at the Matjiesrivier Nature Reserve research base (elevation 743 m), dropped to as low as -7°C in winter, and reached 47°C in summer (Q. Martins unpubl. data). The Cederberg is predominantly a winter rainfall area with sporadic thunderstorms during the summer months. Over a 10-year period, the average annual rainfall was 179 mm (214±22 mm) for the Karoo (Matjiesrivier Nature

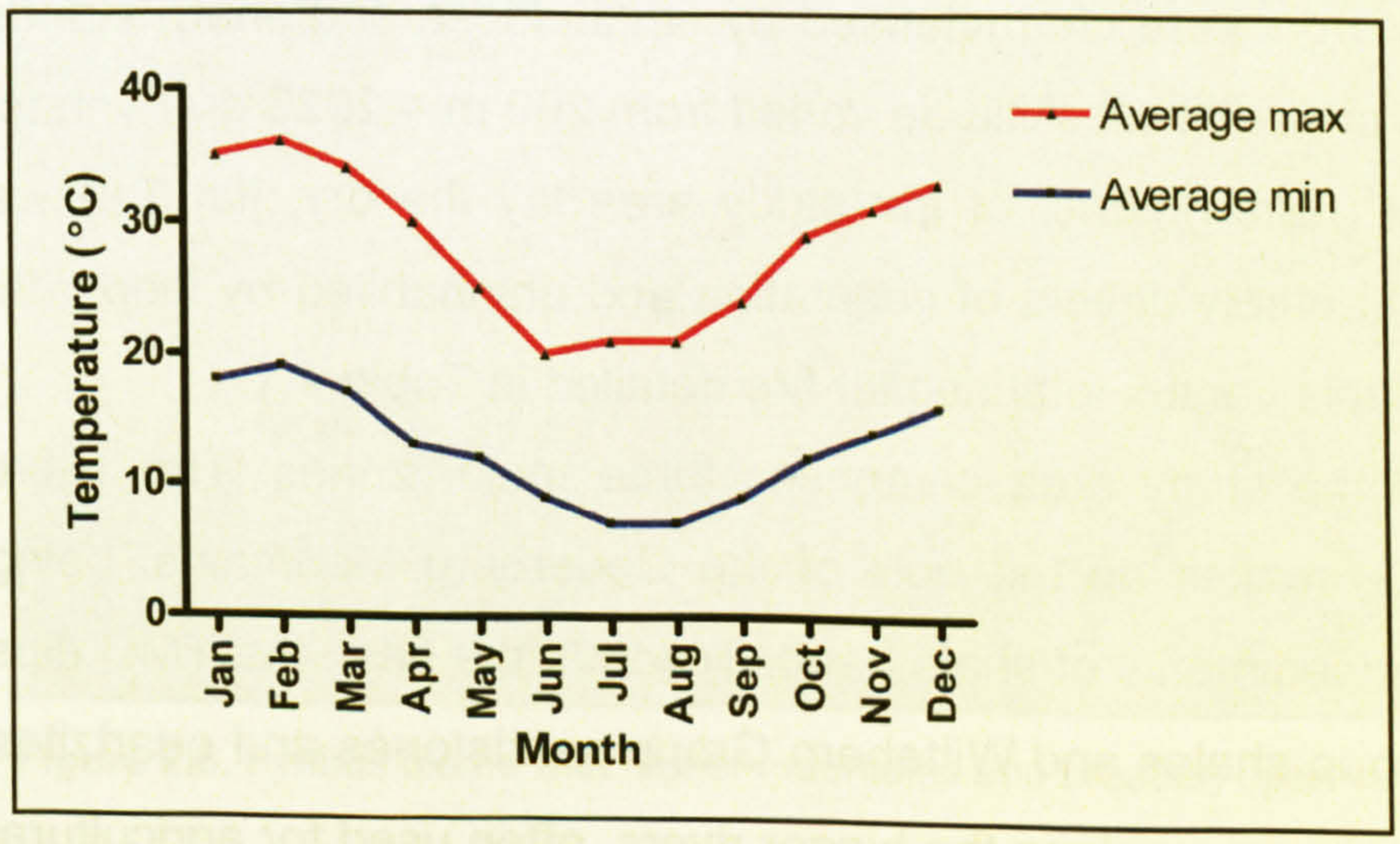


Figure 2.3. Average minimum and maximum temperatures for the Cederberg from 2004-2009, taken at the Clanwilliam weather station).

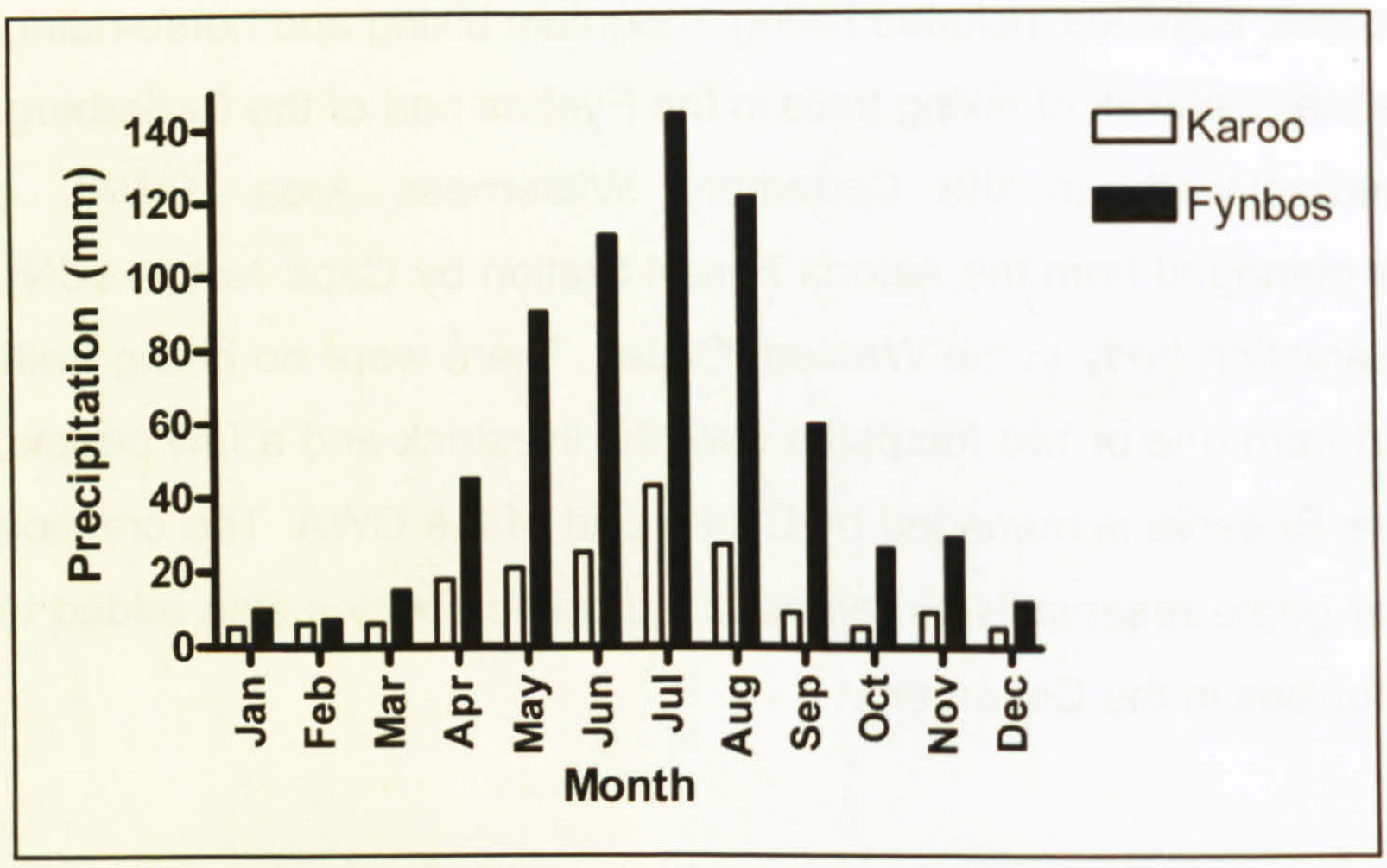


Figure 2.4. Average rainfall taken over 10 years (2000-2009) in the Karoo (data from Matjiesrivier Nature Reserve) and Fynbos (data from Algeria Forest Station).

Reserve) and 669 mm (669±60 mm) for the Fynbos (Fig. 2.4) (Algeria Forest Station, Cape Nature; 532 m). Snow was recorded every winter on higher ground, mostly melting within two weeks of snowfall.

2.3. Topography and geology of the Cederberg

The topography in both Karoo (Fig. 2.5) and Fynbos (Fig. 2.6) biomes consisted of rugged sandstone and shale mountains interspersed with open valleys and deeply incised ravines ('kloofs'). In the Fynbos, the mountains were larger, with bigger and broader U-shaped valleys, whereas the Karoo had rough, steep V-shaped kloofs formed along perennial or non-perennial rivers, as well as larger, flat open areas. Slopes in the Karoo were characterised by small, loose and sharp stones making walking in this area difficult. Altitude varied from 200 m – 2026 m (Fynbos) and 258 m – 1446 m (Karoo). East of the study area lay the dry, flat Tankwa Karoo, an area almost entirely devoid of vegetation and uninhabited by leopards. The proportion of available versus total habitat are detailed in Table 4.1.

The geology of the study area comprises three major zones. The Table Mountain Group (TMG) makes up the bulk of the Cederberg Mountains, being interspersed with softer sediments of shale band. Towards the east, the TMG dips beneath Bokkeveld Group shales and Witteberg Group sandstones and quartzites (Fig. 2.7). Alluvial deposits occur along the bigger rivers, often used for agricultural purposes; it is here that vineyards, olives and citrus are grown.

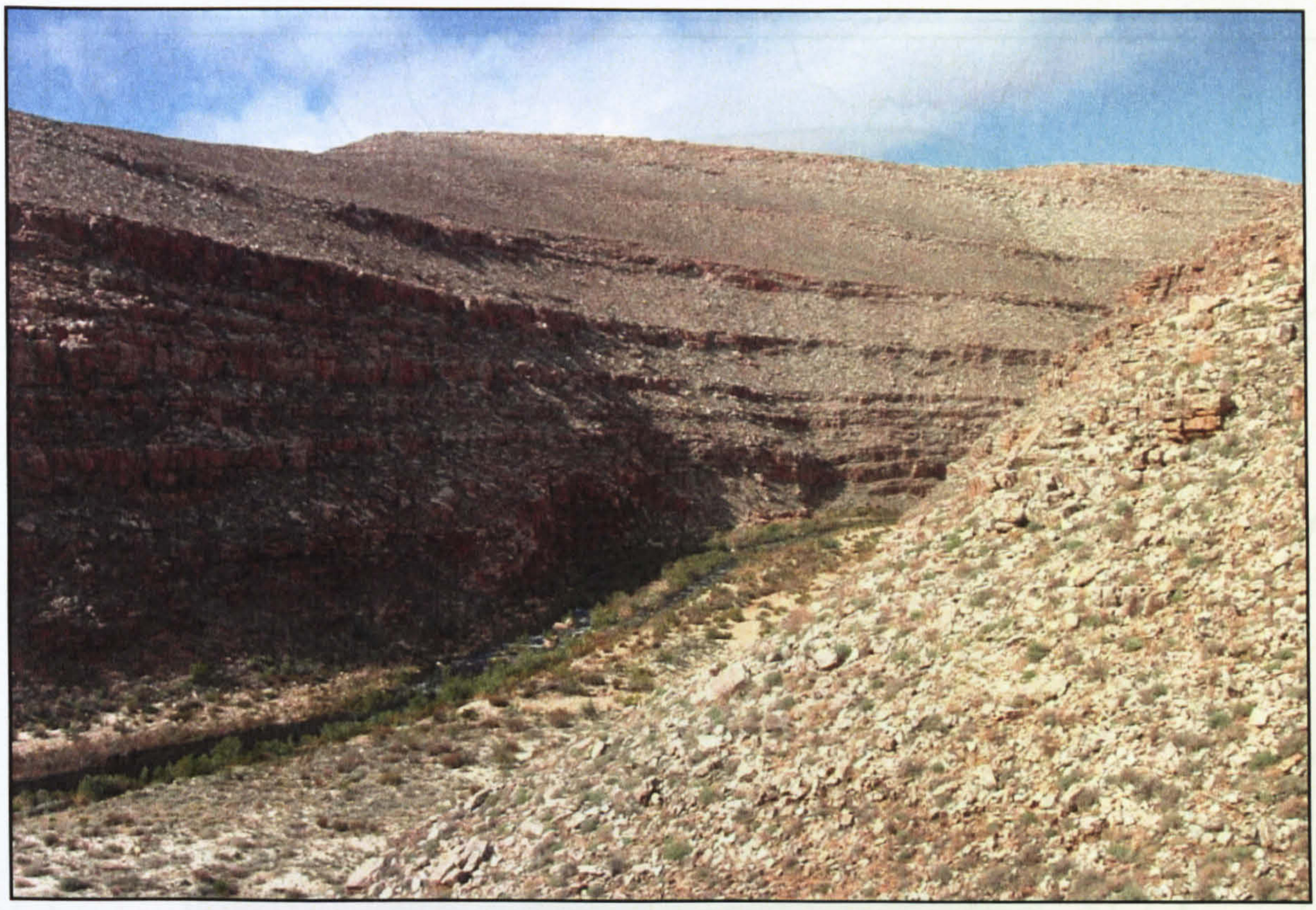


Figure 2.5. Karoo biome with steep, rugged slopes along steep V-shaped kloofs.

Figure 2.6. Fynbos biome with higher mountains and broader, open valleys.

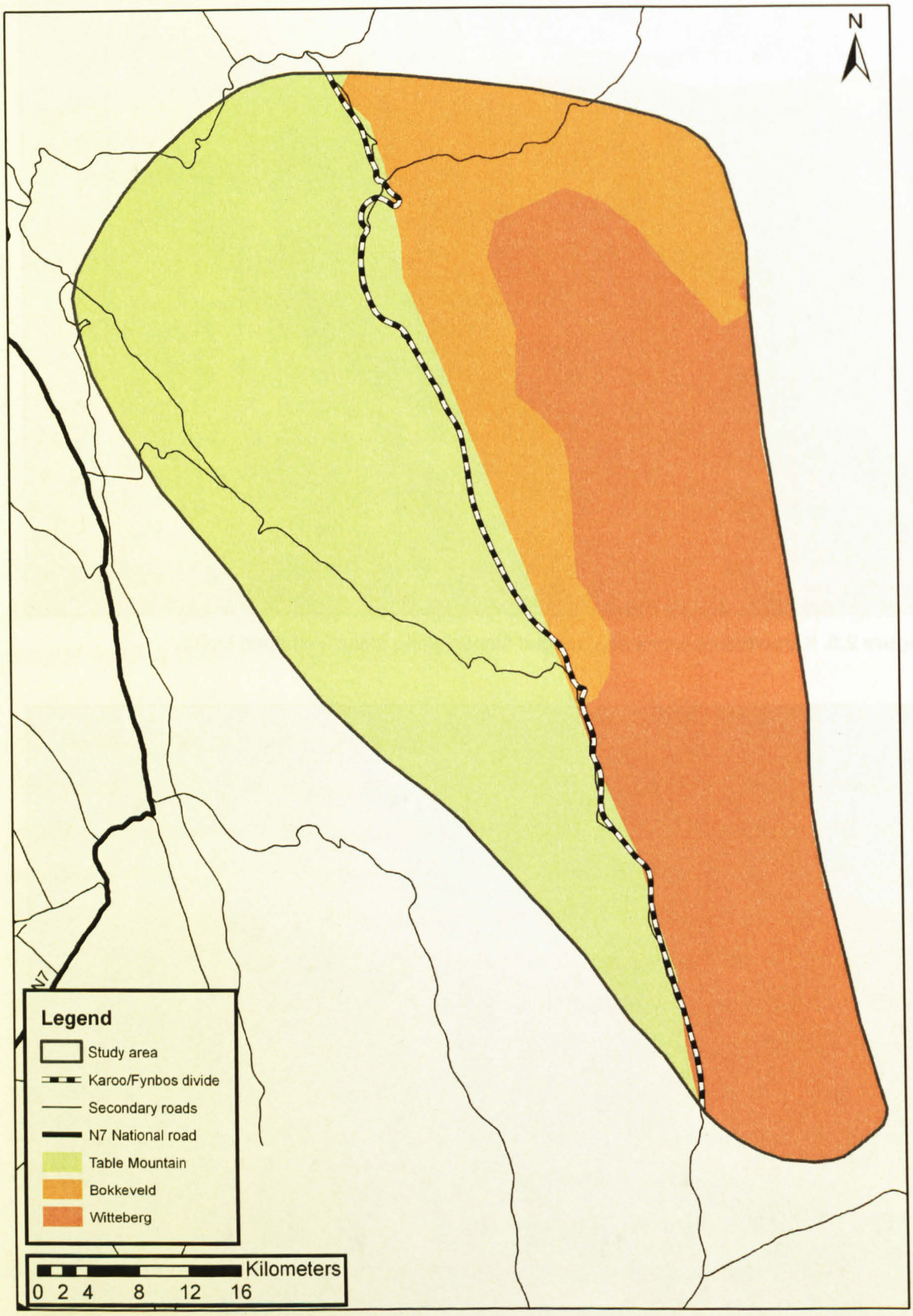


Figure 2.7. Geology of the Cederberg Mountains. The Table Mountain Group forms the major geological formation on the Fynbos side of the Cederberg. East of the vegetation divide, the Bokkeveld and Witteberg formations dominate.

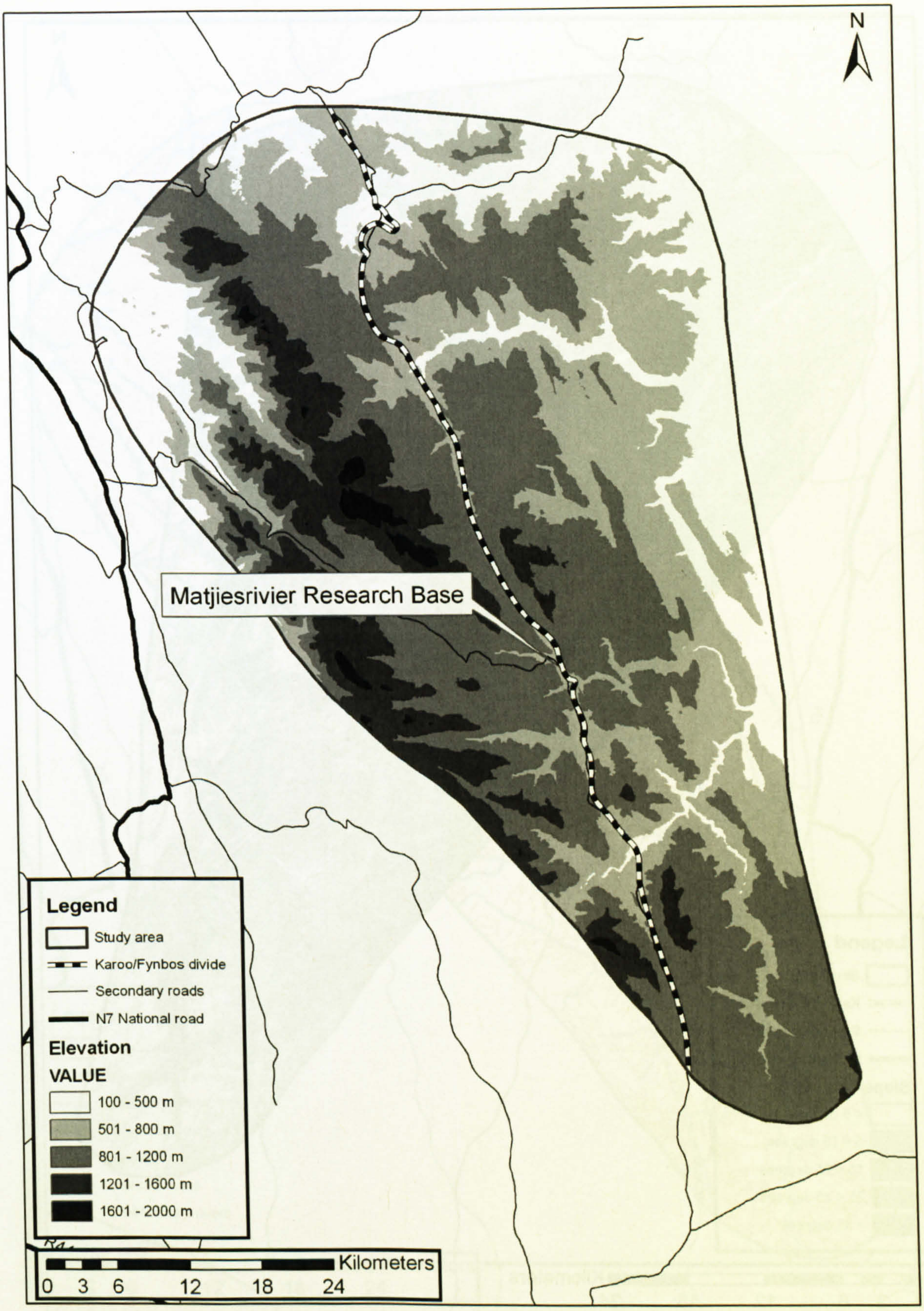


Figure 2.8. Elevation map of the Cederberg study area.

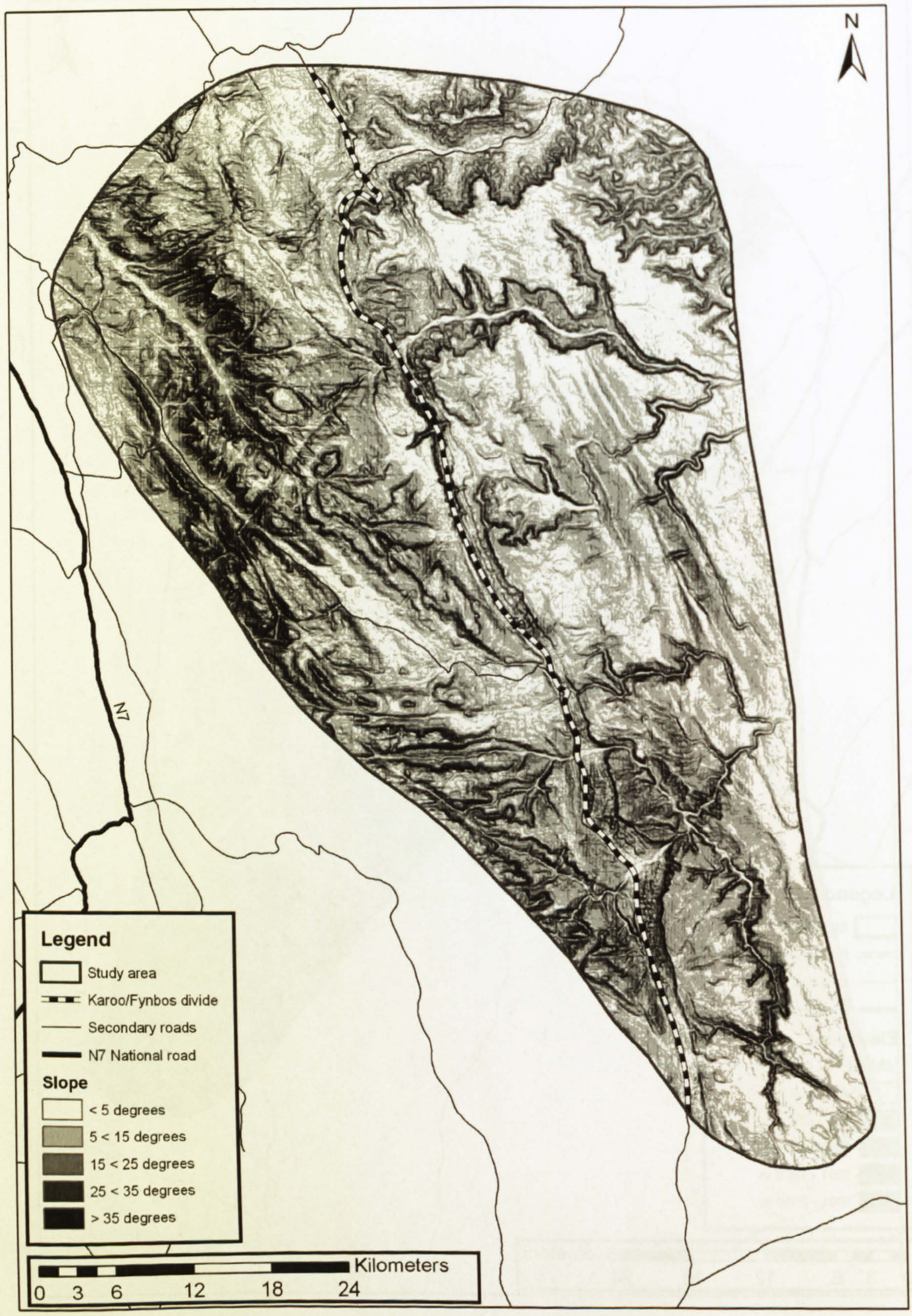


Figure 2.9. Map of the Cederberg study area showing the five categories of slope.

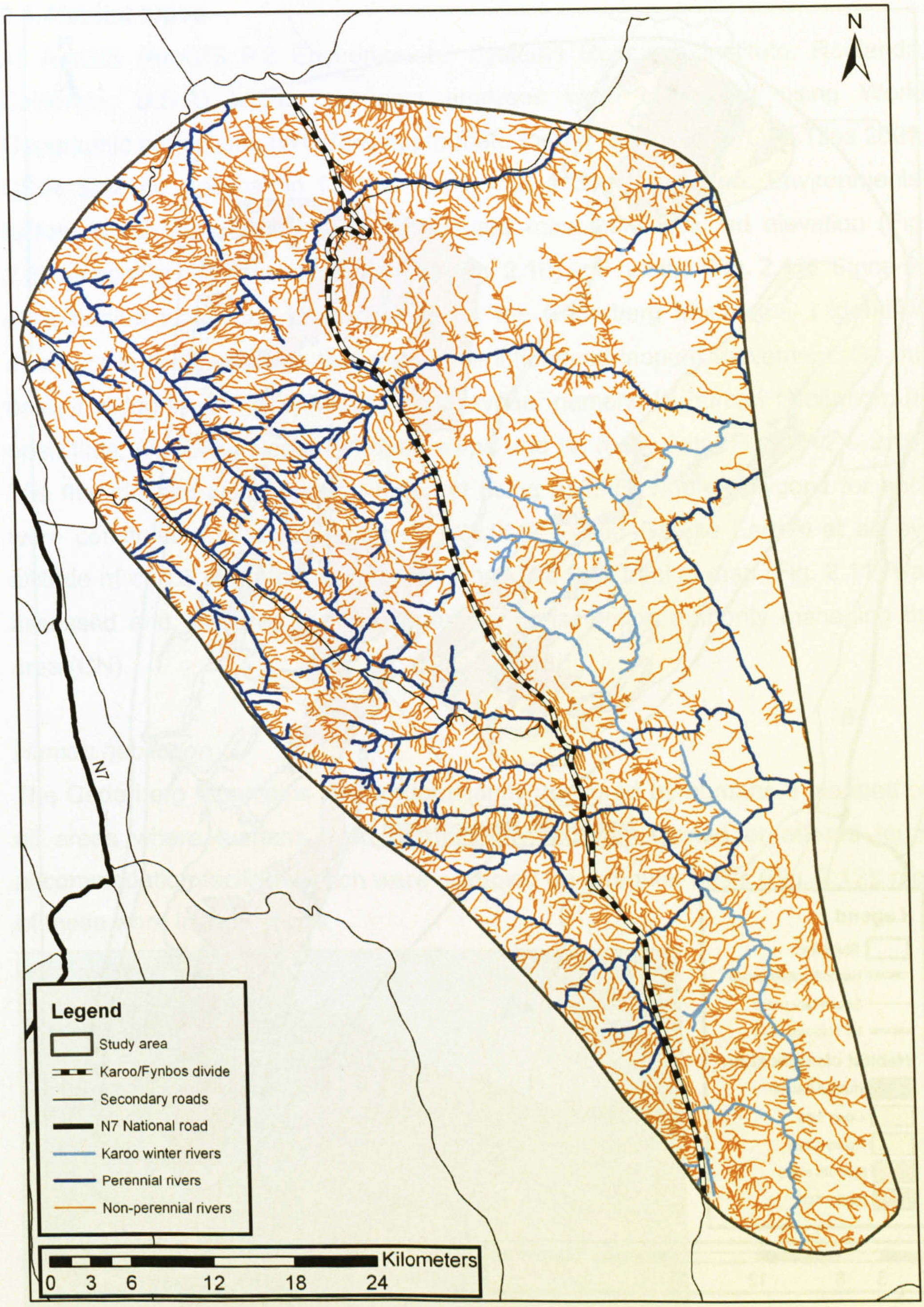


Figure 2.10. Rivers of the Cederberg study area.

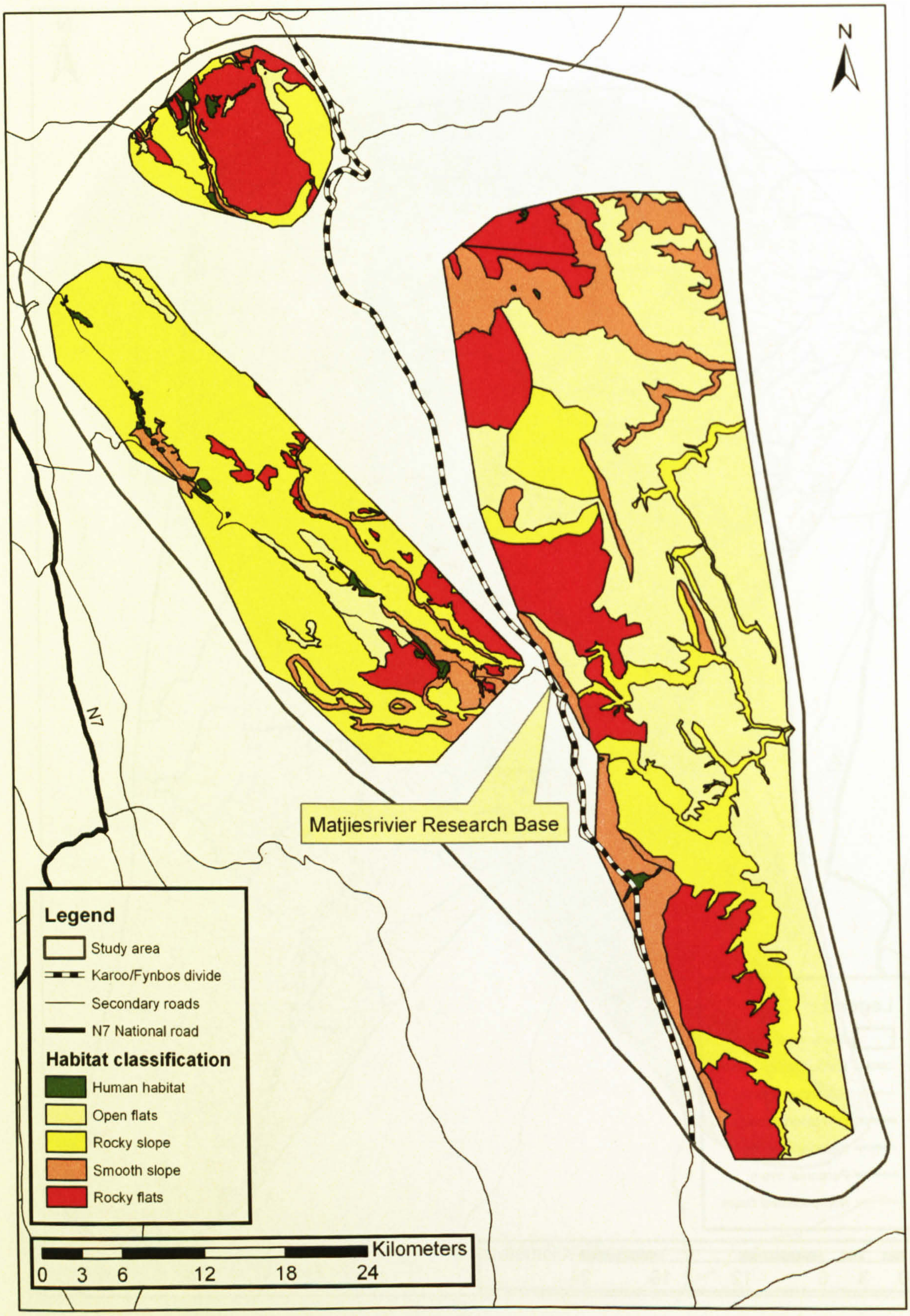


Figure 2.11. Habitats of the Cederberg Mountains in the areas where I had contiguous collared leopard populations, based on the 95% MCPs of their individual ranges.

2.4. Habitat types

All ArcGIS (ArcGIS 9.2 Environmental Systems Research Institute, Redlands, California, U.S.A) habitat mapping analyses were conducted using World Geographic projections (WGS84) appropriate for this area and SPOT5 Tiles 2007, CSIR Satellite Application Centre maps with a 30m resolution. Environmental factors which may have influenced leopard movement included elevation (Fig. 2.8), slope (Fig. 2.9), distance to rivers (Fig. 2.10) and habitat (Fig. 2.11). Since no clear habitat types had been defined for the Cederberg Mountains, I identified elements in the landscape that may have influenced leopard movement. On this basis I recognised five different habitat types, namely: (i) human habitation; (ii) open flats; (iii) rocky slope; (iv) open slope and (v) rocky flats (Figs 2.12 – 2.16). The five classes were mapped by hand using ArcGIS, where polygons for each were constructed at a resolution of 1:20,000. I used Google Earth® at an eye altitude of *c.* 3.5 km to confirm terrain type. The final habitat map (Fig. 2.11) was assessed and validated by the Cederberg conservation authority managing the area (CN).

Human habitation

The Cederberg Mountains are predominantly unaltered by humans. I mapped out all areas where humans lived permanently, actively farmed or offered tourist accommodation facilities which were occupied on a regular basis (Fig. 2.12); most of these were in the Fynbos.

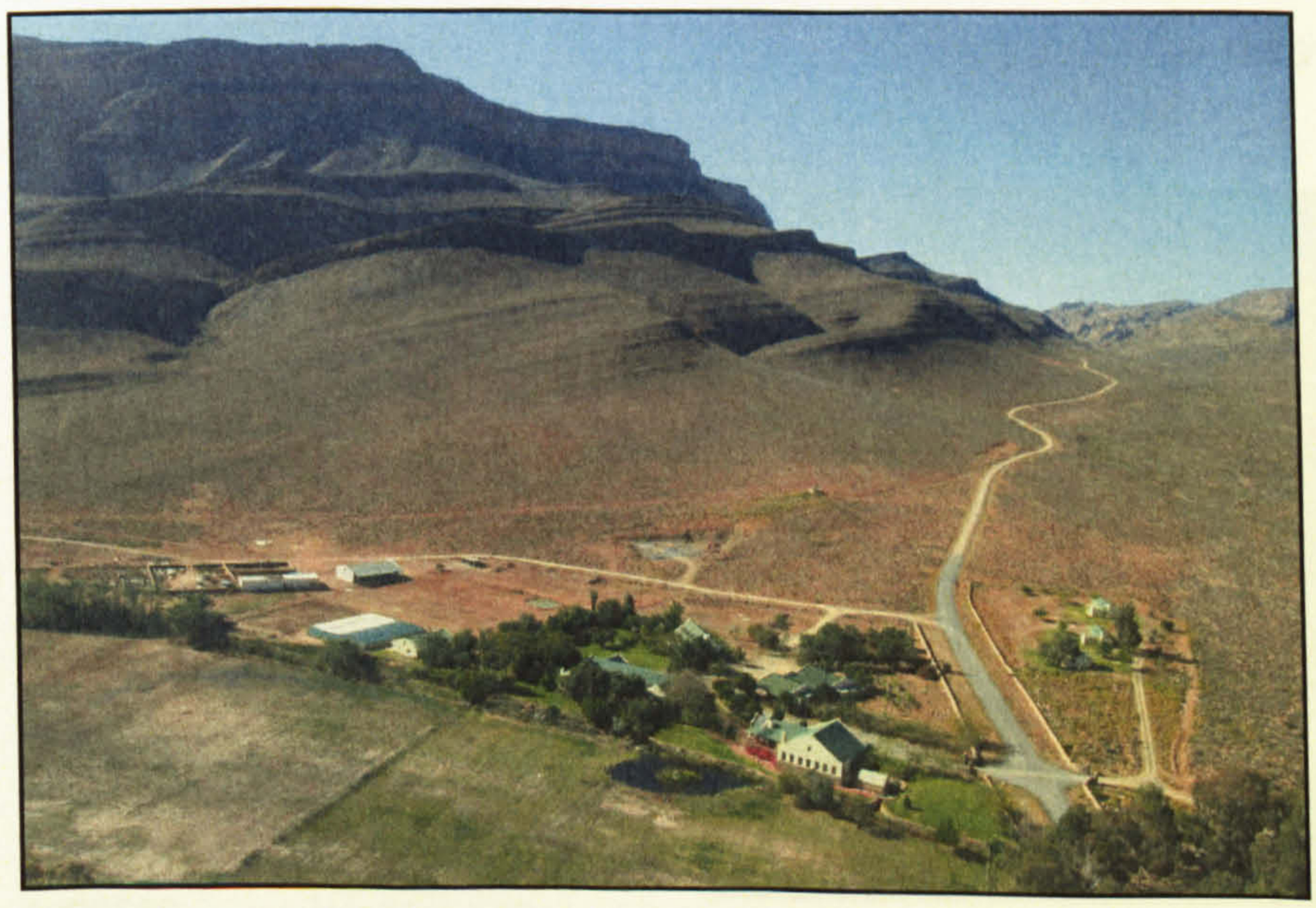


Figure 2.12. Human habitat including lucerne fields, horse paddocks and tourism accommodation.

Open flats

I considered all relatively flat areas with an absence of rocky outcrops or large boulders as 'open flats' (Fig. 2.13). Vegetation cover was not considered a factor, as cover was sparse, and constantly changing as a result of the fire-driven system in the Cederberg. Because wetlands were uncommon in the Fynbos and non-existent in the Karoo, the few small wetlands were included in this habitat type.

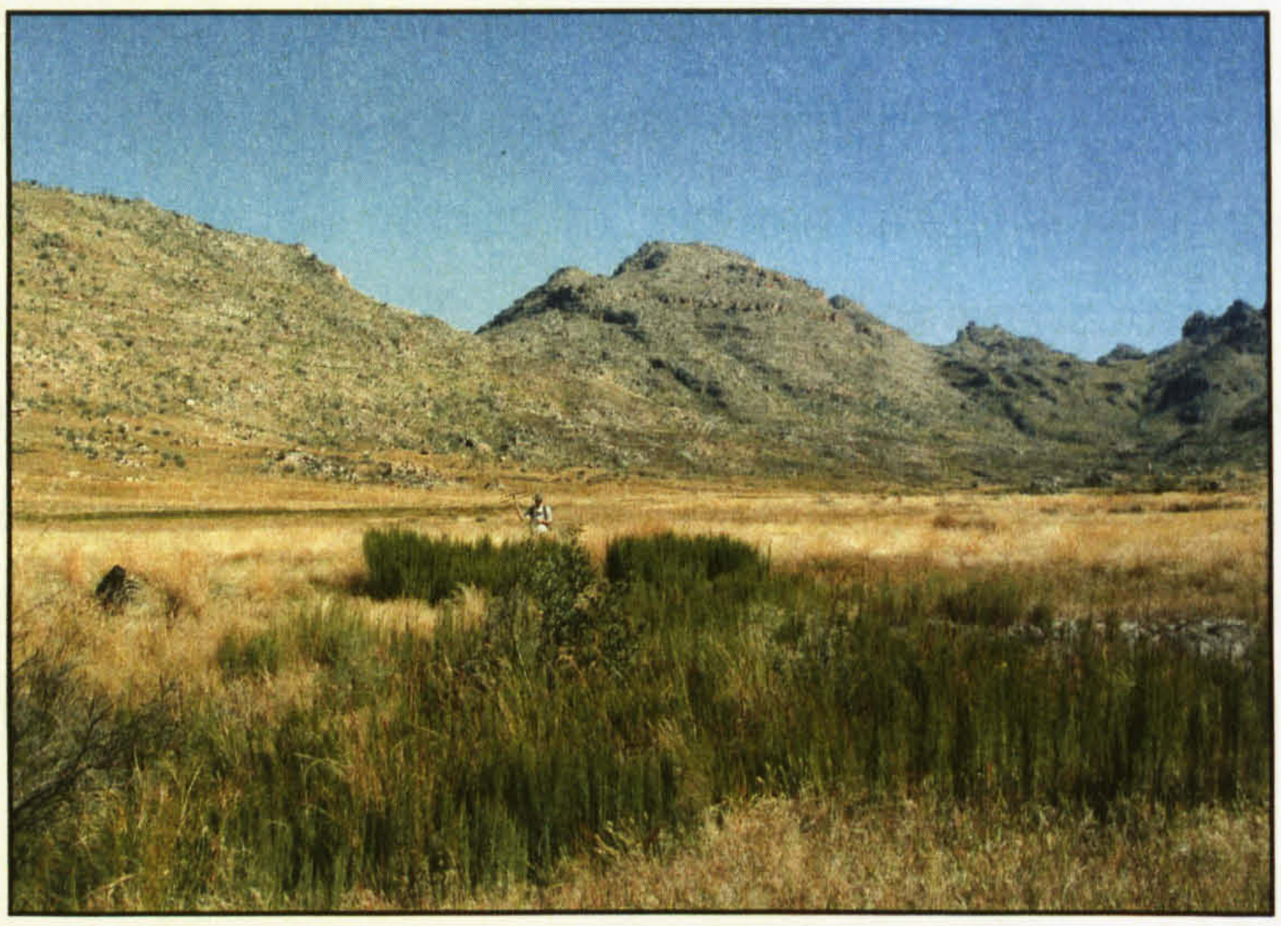


Figure 2.13. 'Open flats' surrounded by mountains with 'Rocky slope'.

Rocky slope

Rocky slope was the dominant habitat type in the mountainous Fynbos part of the Cederberg. It was characterised by rocky and rough or rugged slopes, with or without significant vegetation cover (Fig. 2.14). Many of these slopes had large boulders and rocks strewn across them.

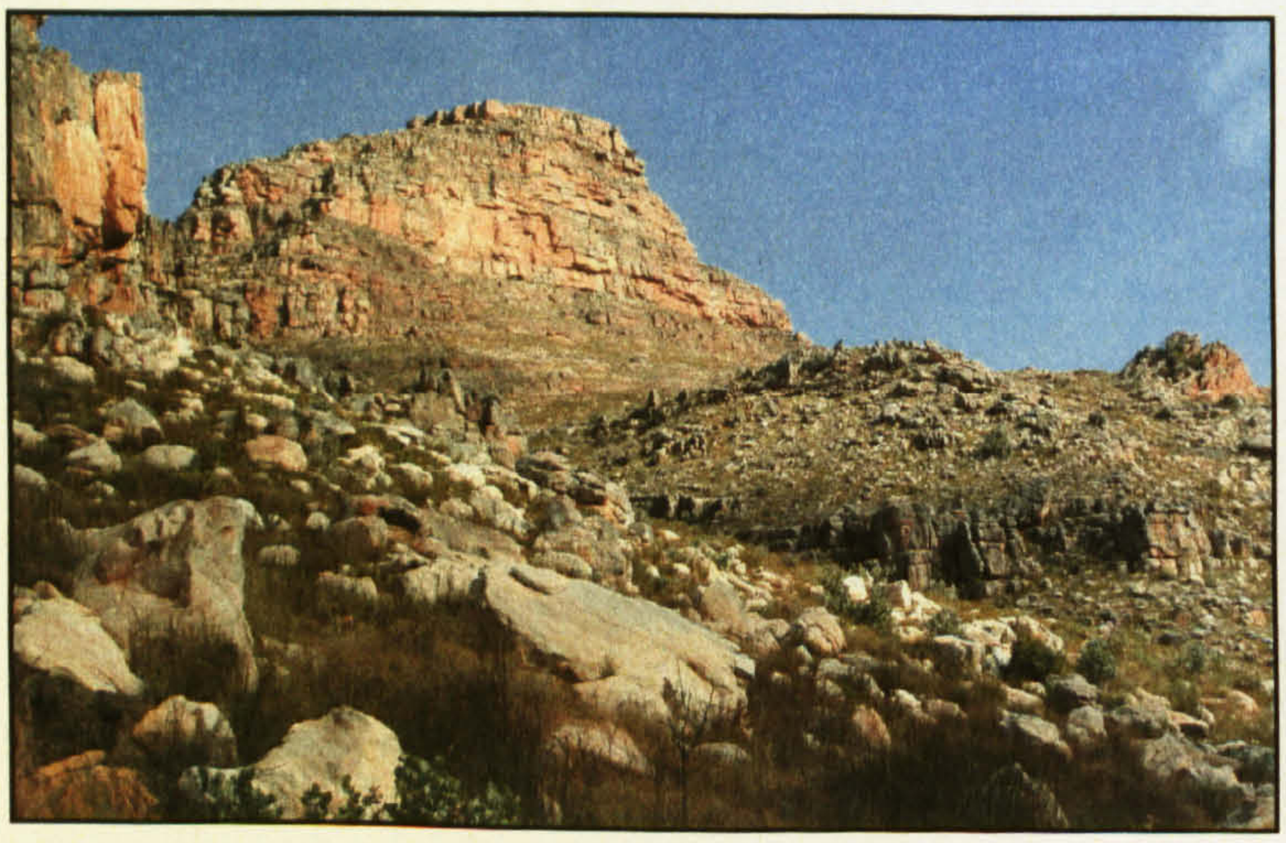


Figure 2.14. 'Rocky slope' with large boulders.

Smooth slope

The shale bands occurring in the Cederberg often formed smooth, open slopes with little cover from rocks, boulders or bushes (Fig. 2.15). Many of these occurred at high altitude.

Figure 2.15. 'Smooth slope' with very few large boulders on the slope.

Rocky flats

Rocky flats occurred where the *c.* 400 million-year old Table Mountain Group sandstone had been severely eroded by wind, water and glacial action, deforming flat, rocky plateaus and creating a rough, jagged landscape with small gulleys, small rock outcrops and unusual features such as holes in the rock (Fig. 2.16).

Figure 2.16. 'Rocky flats' showing effects of considerable erosion, with gulleys and uneven surfaces.

2.5 Vegetation, fauna and flora

The Cederberg occurs entirely within the Cape Floralistic Region, the smallest of the six Floral Kingdoms in the world. There were two biomes; the Fynbos biome and the Succulent Karoo biome (Mucina & Rutherford, 2006) (Fig. 2.17). The 3000 km^2 study area was comprised equally of Fynbos and Karoo biomes. Fynbos vegetation consisted of small shrubs, grass-like 'restios' interspersed with small trees (*Protea* species) and remnant populations of the endemic Clanwilliam cypress tree, whereas the predominant Karoo vegetation, Dry Karoo Shrubland, was dominated by small shrubs (<1 m high) and succulents (Mucina & Rutherford, 2006). Further east, Karoo vegetation became more sparse entering the Tankwa Karoo. The Fynbos was more vegetated than the Karoo, although small trees or shrubs occurred along permanent rivers in the Karoo.

Most mammals in the study area were cryptic and/or nocturnal, and rarely observed. However, a camera-trapping study in the Karoo revealed 34 mammal species, including five small antelopes with a mass <25 kg. Of these, grey rhebok *Pelea capreolus* was the largest, averaging 21 kg (Skinner & Smithers, 1990) and Cape grysbok *Raphicerus melanotis* the smallest, averaging 10 kg. My camera-trapping study (see Chapter 5) showed that, of 773 photographic captures of small antelopes, 73% were klipspringer *Oreotragus oreotragus* (average mass 12.5 kg), 20% grysbok, 6% grey rhebok and <1% steenbok *Raphicerus campestris*. While camera data were not available for the Fynbos, sighting data suggest that klipspringer were most common. Some of the larger herbivores historically present, such as gemsbok *Oryx gazelle*, springbok *Antidorcas marsupialis* and Cape mountain zebra *Equus zebra*, had been reintroduced locally on private game reserves. Due to the cryptic nature of many animals, some species, such as black-backed jackal were not encountered during the course of the study although they were captured on camera trap photographs.

Despite the Fynbos providing poor grazing for livestock and indigenous ungulates (Johnson, 1992), intensive farming with small livestock was prevalent in the Cederberg over 40 years ago, when 26,000 sheep and goats grazed in the mountains, being moved from the summer grazing in the Fynbos 'sourveld' to the palatable 'sweetveld' of the Karoo in winter. Evidence of overgrazing is still seen in the Karoo, and it may take decades for this sensitive habitat to recover from overgrazing (Boardman, 2010).

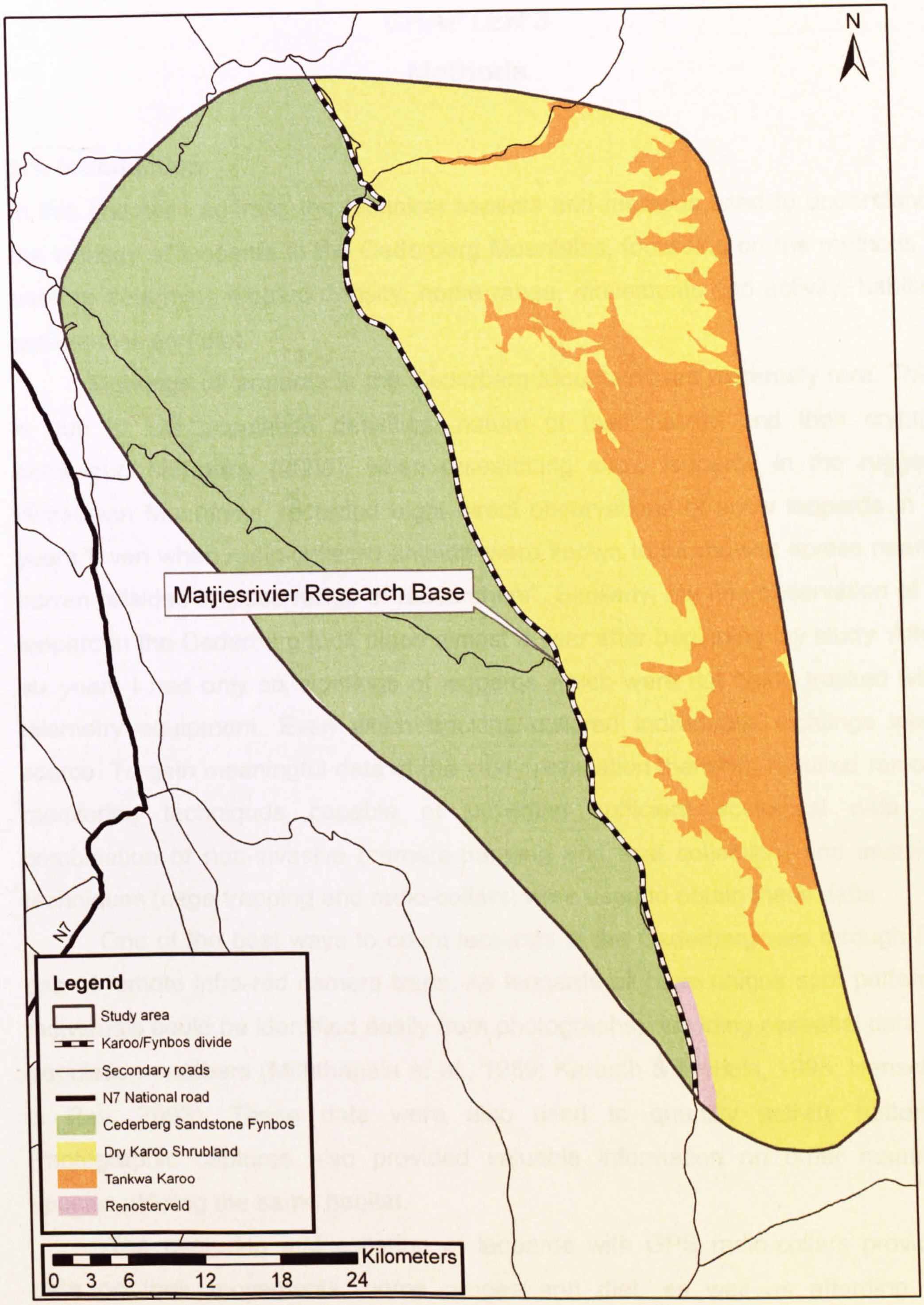


Fig. 2.17. Vegetation of the Cederberg showing the Cederberg Sandstone Fynbos dominating the west, while Dry Karoo Shrubland dominated the east. Although Renosterveld could be found interspersed with Karoo and Fynbos vegetation, the only prominent stand occurred in the south. Tankwa Karoo vegetation occurred in the far east of the study area.

CHAPTER 3

Methods

3.1. Introduction

In this chapter I address the technical aspects and methods used to understand the ecology of leopards in the Cederberg Mountains, focussing on the methods I used to determine leopard density, home range, movements and activity, habitat preferences and diet.

Sightings of leopards in the Cederberg Mountains are extremely rare. This is due to low population densities, nature of their habitat and their cryptic behaviour. McCarthy (2000), when researching snow leopards in the rugged Himalayan Mountains, recorded eight direct observations of snow leopards in 7 years "even when radio-collared animals were known to be moving across nearly barren hillsides in close range of researchers". Similarly, my first observation of a leopard in the Cederberg took place almost a year after beginning my study. After six years I had only six sightings of leopards which were not being tracked with telemetry equipment. Even when tracking collared individuals, sightings were scarce. To gain meaningful data of the study population therefore required remote monitoring techniques capable of providing sufficient ecological data. A combination of non-invasive (camera-trapping and scat collection) and invasive techniques (cage trapping and radio-collars) were used to obtain these data.

One of the best ways to count leopards in the Cederberg was through the use of remote infra-red camera traps. As leopards all have unique spot patterns, individuals could be identified easily from photographs, providing essential data on population numbers (Miththapala *et al.*, 1989; Karanth & Nichols, 1998; Henschel & Ray, 2003). These data were also used to quantify activity patterns. Photographic captures also provided valuable information on other mammal species utilizing the same habitat.

The capturing and collaring of leopards with GPS radio-collars provided data on their movements, home ranges and diet, as well as affording the opportunity to collect genetic material (tissue samples of <8 mm^2 clipped from the ear) (Martins, 2006; A. Ropiquet *et al.*, unpubl. data) and morphological data for comparisons with leopard populations elsewhere.

3.2. Materials and methods

Data were captured in Microsoft® Office Excel® 2007, and statistical analyses were performed using GraphPad Prism version 4.00 for Windows, GraphPad Software, San Diego California USA, (www.graphpad.com). Means are provided with standard errors (±SE).

3.2.1. Field observations of prey

Attempts to determine prey densities in the Cederberg were thwarted by low sample sizes. Animals were either nocturnal, cryptic or in very low densities, making them difficult to detect. I made use of a palm computer with built in GPS (Fujitsu Siemens Computers Pocket LOOX C550) loaded with the wildlife data collecting software Cybertracker™. Although the data capture process was simple and often worked well, problems occurred with obtaining GPS locations, when the unit would freeze. To save battery power, the unit was often only powered to capture a sighting, thus eliminating the recording of entire routes while conducting transects. Ideally each transect (vehicle or foot transect) should be monitored, with regular locations (every *c.* 10 seconds) being taken while in the field. Regardless of the technical difficulties, low numbers of animal sightings made prey surveys difficult. I therefore focussed my prey analysis in the Karoo where I had obtained comparable data using results from camera trap photographic captures (see 3.2.2). I first began using Cybertracker™ in 2006, and included all data from November 2006 – March 2009. Table 3.1 summarises the animals observed on 421 patrols where a combination of vehicle and foot patrols took place.

3.2.2. Use of remote infra-red camera traps

Population estimates

I undertook camera trapping surveys using remote infra-red cameras with heat and motion sensors between 2004 and 2007. I used 40 DeerCam™ 35 mm film cameras (models 100 and 200, DeerCam, Park Falls, WI, USA) using 36-exposure 400 ASA film. Each photograph displayed the date and time of capture (Fig. 3.1). I did four camera surveys in the eastern and southern part of my study area (Fig. 3.2). It was not feasible to conduct camera surveys with film cameras in the northern and western region due to the intensive use of suitable camera-trapping

Table 3.1. Numbers and percentages recorded for species observed on foot or in a vehicle over 421 patrols from November 2006 – March 2009. Groups were recorded as one observation.

Species	Common name	Observations	Percentage (%)
Oreotragus oreotragus	Klipspringer	351	36.9
Procavia capensis	Rock hyrax	207	21.7
Pelea capreolus	Grey rhebok	159	16.7
Papio ursinus	Chacma baboon	62	6.5
Equus zebra	Cape mountain zebra	30	3.2
Lepus capensis / *Lepus saxatilis*	Cape hare / Scrub hare	28	2.9
Antidorcas marsupialis	Springbok	22	2.3
Oryx gazelle	Oryx	22	2.3
Pronolagus rupestris	Smith's red rock rabbit	22	2.3
Silvicapra grimmia	Grey duiker	16	1.7
Aonyx capensis	Small grey mongoose	7	0.7
Felis silvestris	African wild cat	6	0.6
Hystrix africaeaustralis	Cape porcupine	5	0.5
Raphicerus melanotis	Cape grysbok	5	0.5
Caracal caracal	Caracal	3	0.3
Vulpes chama	Cape fox	3	0.3
Genetta genetta	Small spotted genet	1	0.1
Ictonyx striatus	Striped polecat	1	0.1
Mellivora capensis	Honey badger	1	0.1
Orycteropus afer	Aardvark	1	0.1

sites by hikers resulting in film wastage and tampering with cameras (Stuart & Stuart, 1991), making monitoring impossible in these areas.

I conducted a preliminary survey from 8th May to 10th November 2004 to determine camera battery life, whether cameras functioned properly, and whether they were suitably placed for photographing leopards. Camera failures were experienced on cold days due to a power supply problem when photographs were taken using the automatic flash. I modified the camera power source by replacing the two standard AA batteries with two plastic 'dummy' batteries, each with wires leading to a rechargeable 6V lead-acid battery. Camera voltage was regulated by a rheostat to obtain a constant voltage of 3.3V.

The design for surveys 1 (November 2004 – March 2005) and 2 (May 2005 – September 2005) was based on: (i) the survey area determined by the estimated home range of female leopards as recommended by Rabinowitz & Nottingham (1986); (ii) the initial hypothesis that different land-use types had

Figure 3.1. Camera trap photograph of a Cederberg leopard showing date and time of capture.

an effect on leopard densities; and (iii) seasonal variation presumed to affect leopard movements in the study area. As no previous data were available on female leopard movements in the Cederberg, camera spacing and survey grid size were calculated using home range estimates of male leopards (51±9 km^2) (Norton & Henley, 1987). Assuming two to three females inhabited each male range (Hamilton, 1976), I allowed for a minimum home range of a female leopard of *c.* 25 km^2. A maximum distance of 3 km between camera stations ensured no gaps where leopards had a zero chance of being detected when moving through the area (Karanth & Nichols, 2000, 2002; Maffei *et al.,* 2004) and that the study area was large enough to contain at least parts of the home ranges of several individuals (Henschel & Ray, 2003).

Survey 1 began in summer on the 11th November 2004 and survey 2 in winter on the 15th May 2005; each lasted 120 days. Three land-use types were investigated: (i) livestock farming (farming with small or large stock); (ii) game farming, i.e. areas used for the re-introduction of ungulate game species, such as springbok, with no livestock; and (iii) conservation land-use areas that had no livestock or no re-introduced game (Fig. 3.2). Each of the three land-use types was surveyed during each survey, with twenty camera stations for 40 successive

days before cameras were collected and moved to the next land-use type. The collection and repositioning of the cameras took two to four days (Table 3.2). I had one extra person help me when removing or setting up cameras in the livestock farming area, as this required the most hiking. Cameras in the game farming area were mostly accessible by 4x4 vehicle over rough jeep tracks. Although most camera stations were placed in the low-lying river regions or kloofs, accessing them often meant hiking over steep terrain with loose rock.

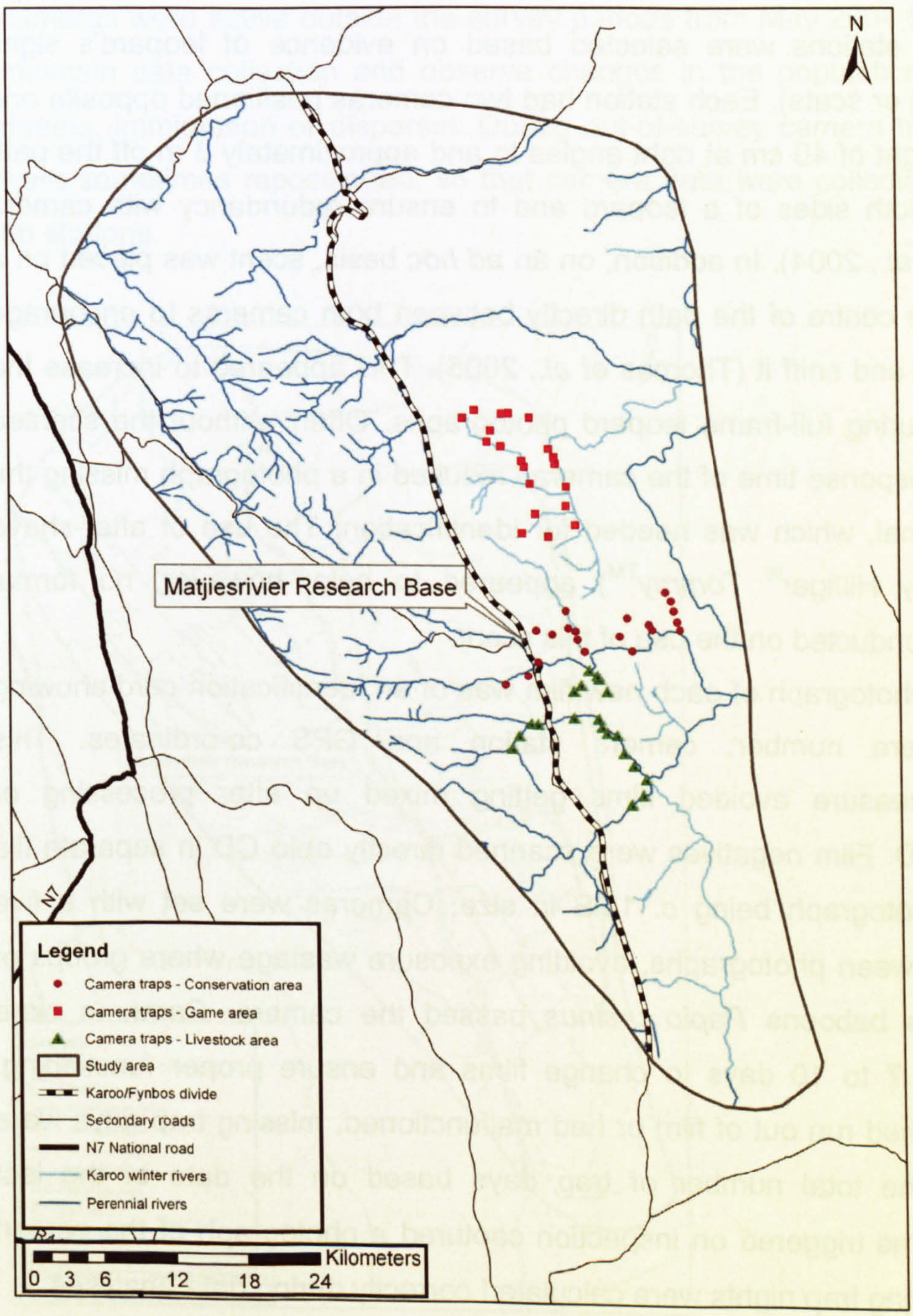


Figure 3.2. Cederberg camera trap surveys 1 and 2.

Table 3.2. Camera-trapping survey design for surveys 1 and 2 including length of surveys, land-use, season and starting date.

Survey	Start date	Days	Land-use	Season
1	11/11/2004	1 - 40*	Livestock	Summer
1	24/12/2004	44 - 84*	Game	Summer
1	04/02/2005	88 - 128	Conservation	Summer
2	15/05/2005	1 - 40*	Livestock	Winter
2	27/06/2005	44 - 84*	Game	Winter
2	09/08/2005	88 - 128	Conservation	Winter

*There were 2-4 days between each survey for moving cameras

Cameras stations were selected based on evidence of leopard's signs (tracks, scraping or scats). Each station had two cameras positioned opposite one another at a height of 40 cm at right angles to and approximately 3 m off the path to photograph both sides of a leopard and to ensure redundancy with camera failure (Silver *et al.*, 2004). In addition, on an *ad hoc* basis, scent was placed on a dried stick in the centre of the path directly between both cameras to encourage leopards to stop and sniff it (Thomas *et al.*, 2005). This appeared to increase the chances of capturing full-frame leopard photographs. Often, without the scented stick, the slow response time of the cameras resulted in a photograph missing the flank of the animal, which was needed for identification. The use of after-shave cologne (Tommy Hilfiger® *Tommy*™) appeared to help; however, no formal analyses were conducted on the use of this scent.

The first photograph of each new film was of an identification card showing the date, camera number, camera station and GPS co-ordinates. This precautionary measure avoided films getting mixed up after processing or scanning onto CD. Film negatives were scanned directly onto CD in separate file folders, each photograph being *c.* 1MB in size. Cameras were set with a five minute delay between photographs, avoiding exposure wastage where groups of animals such as baboons *Papio ursinus* passed the camera. Cameras were monitored every 7 to 10 days to change films and ensure proper functioning. Where cameras had run out of film or had malfunctioned, missing trap days were deducted from the total number of trap days based on the date of the last exposure. Cameras triggered on inspection captured a photograph of the person checking it, ensuring trap nights were calculated correctly during data analyses.

The design for surveys 3 and 4 was altered based on the results of surveys 1 and 2. Results from the early surveys showed that leopard ranges were far bigger than expected, with one male occurring in the extremities of the whole area surveyed. As my defined land-use areas were too small, I compensated for this by incorporating all three land uses into one complete survey area for surveys 3 and 4, creating 17 permanent camera stations, with cameras no more than 9 km apart (Fig. 3.3). Survey 3 ran for 120 days in winter 2006 (May – September), survey 4 for 120 days in summer 2006/2007 (November – March). Between 5 and 40 cameras were active outside the survey periods from May 2004 to March 2010 to maintain data collection and observe changes in the population such as births, deaths, immigration or dispersal. During out-of-survey camera trapping, cameras were sometimes repositioned, so that camera data were collected from a total of 66 stations.

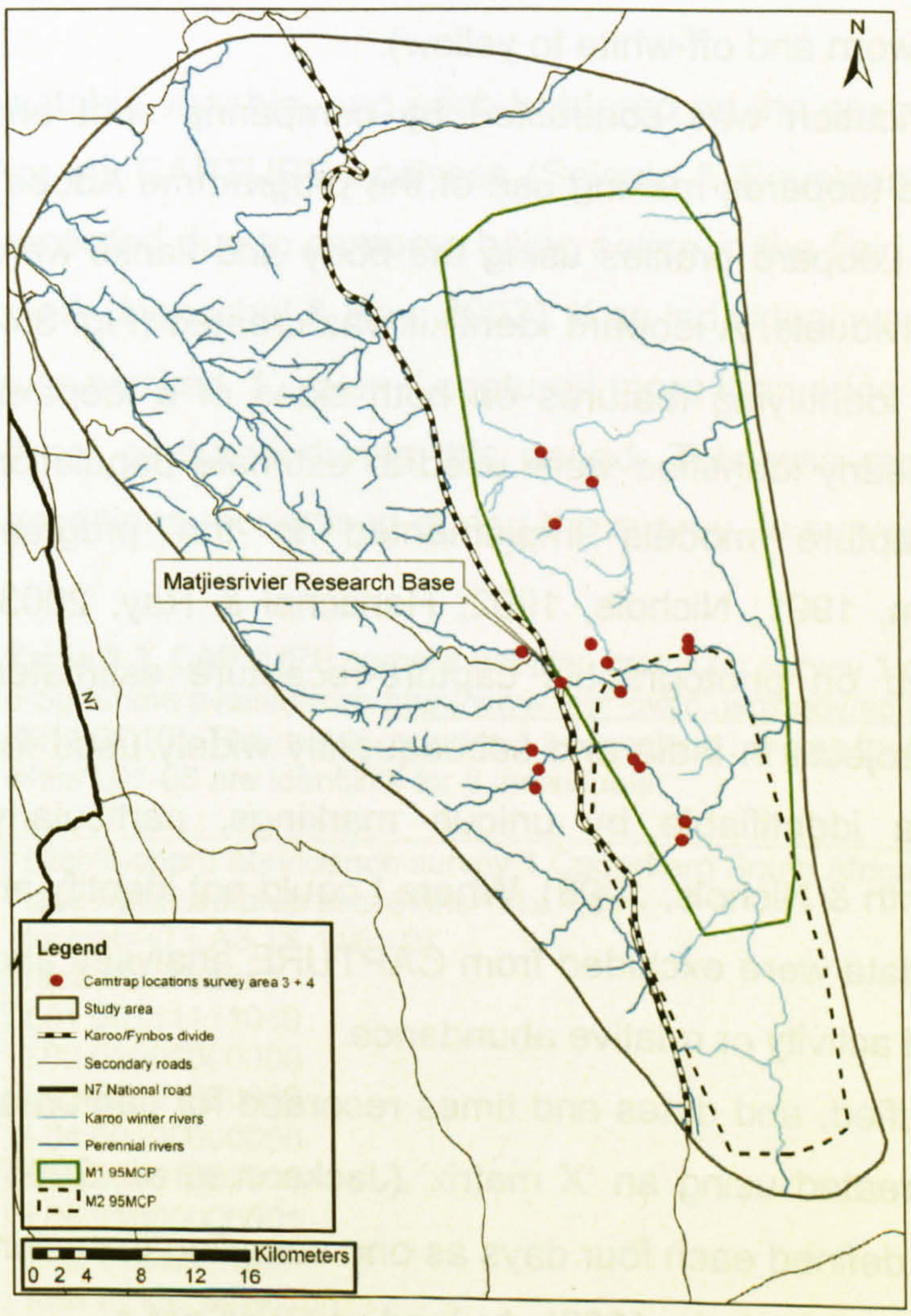


Figure 3.3. Cederberg camera trap surveys 3 and 4. The 95% MCP home ranges for Karoo male leopards M1 and M2 are also shown.

All photographs, irrespective of image results, were recorded in an Excel camera trap file with a unique sheet for each camera station. Leopard photographic captures included information on the identity, sex and its age estimate. Adult male leopards were often easy to sex, either by observation of testes, or by their larger head, shoulders and neck region. Females and sub-adults were sometimes confused until sufficient photographic recaptures over time or physical capture of the individual provided the information necessary for classification. One sub-adult male (*c.* 1.5 yrs old) was misidentified as a female when first photographed in May 2005, until he was captured in August 2005. Aging of leopards of a known sex from camera photographs was difficult and limited to juvenile (<1 yr; rough, shaggy coat); sub-adult (1 to <3 yrs; medium-to-smooth coat; small build for males; lack of regular recaptures; aged by tooth wear and colouration if leopard was physically captured) and adult (≥3 yrs; regular photographs of individual in an area over an extended period of time; males heavy set; females smooth coat; teeth worn and off-white to yellow).

Individual leopard identification was conducted by comparing spot and rosette patterns of photographed leopards making use of the programme Adobe® Photoshop® CS2 version 9.0.2. Leopard profiles using the body and flanks were easiest to compare between individuals. A leopard identikit was created (Fig. 3.4) showing, where possible, clear identifying features on both sides of a leopard. Individuals photographed and clearly identified were used to estimate population abundance through mark–recapture models implemented in the program CAPTURE (Rexstad & Burnham, 1991; Nichols, 1992; Henschel & Ray, 2003; Maffei *et al.*, 2004). This relied on photographic capture-recapture estimates developed for tiger monitoring projects in India and subsequently widely used for many cryptic and elusive taxa identifiable by unique markings, particularly carnivores (Karanth, 1995; Karanth & Nichols, 1998). Where I could not identify an individual from the photograph, data were excluded from CAPTURE analyses and only used for analyses of leopard activity or relative abundance.

Once leopards were identified, and dates and times recorded for captures, a leopard capture history was created using an 'X matrix' (Jackson *et al.*, 2005) (Table 3.3). In surveys 1 and 2, I defined each four days as one sampling occasion due to low recapture rates (Karanth & Nichols, 1998). As land use was not a

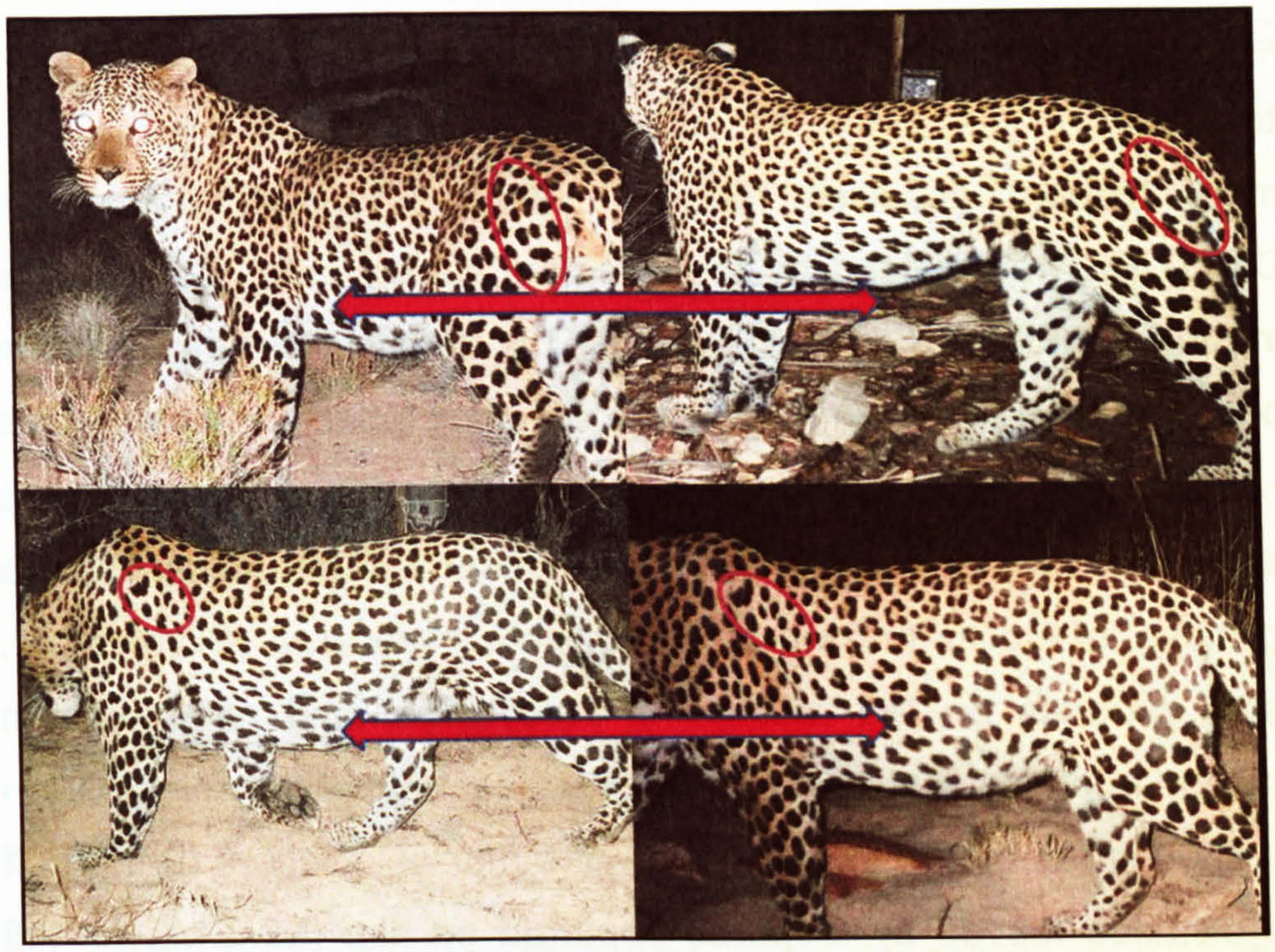


Figure 3.4. Matching leopards using spot patterns. Top photographs of M1, bottom photographs of M2.

suitable variable, and each bordered on the next, I pooled data in surveys 1 and 2 for my CAPTURE analyses (Soisalo & Cavalcanti, 2006). Eleven occasions were recorded due to cameras being active in the field during collection after the 40-day mark (Henschel & Ray, 2003). If an individual was recorded during an 'occasion', it was marked '1', even if captured more than once during this 4 day period, and '0' if not captured during this period. This was repeated for each individual for all occasions recognised during the survey. In surveys 3 and 4, I grouped occasions

Table 3.3. CAPTURE camera trapping matrix for survey 1 generated by internet based CAPTURE programme available on http://www.mbr-pwrc.usgs.gov/software/capture.html (accessed on the 29/09/2010). The matrix includes 11 occasions ranging for 0 = no capture and 1 = leopard capture, while L01-06 are identikits for 6 individuals.

```
title='leopard abundance survey 1 Cederberg South Africa'
task read captures occasions=11x matrix
format='(T1,A3,1X,11F1.0)'
read input data
L01 00111111010
L02 01000000000
L03 00001000000
L04 00100000000
L05 00001000000
L06 01000000001
task closure test
task model selection
task population estimate all
```

as 1 occasion = 10 days due to the surveys being longer and recaptures using 4-day occasions too low.

To estimate leopard densities for each survey, leopard abundance calculated by CAPTURE was divided by the effective survey area. Calculations were made using the formula D = N/A(W), where D is density, N the population size from the program CAPTURE and A(W) the resulting effective survey area sampled which included a boundary strip (Henschel & Ray, 2003). The effective survey area was calculated by adding a circular buffer around each camera station, merging these in ArcGis to form the effective survey area (Silver *et al.*, 2004). Buffer size depends on the method of calculation, and can result in considerable variation in effective survey size and, hence, animal densities (Dillon & Kelly, 2008). I chose to compare four methods of buffer calculation: (i) the half mean maximum distance moved by leopards captured on film (MMDM); (ii) full mean maximum distance moved as captured by camera traps (FMMDM); (iii) the average MMDM as determined by GPS-collared animals divided by two (i.e. the home range radius); and (iv) radius of mean actual home ranges as determined by GPS radio tracking of individuals within the survey area using $A= \pi r^2$, where A = 95% MCP home range area and *r* = the buffer width (Figs 3.5 and 3.6).

Prey species in the Cederberg were not individually identifiable, making density estimates very difficult. So instead, photographic capture rates were compared between species, providing a rudimentary estimate of relative prey abundance (Stein *et al.*, 2008) within the same habitats where leopards were photographed. The limitations of cameras are that they are only able to record animal movement within *c.* 10 m at their fixed point. Since cameras were deployed in areas thought suitable for leopards, species inhabiting other areas, such as bat-eared foxes *Otocyon megalotis*, were not recorded by cameras during the 4 surveys.

Total photographic captures, for leopards as well as other mammals, were calculated as one photographic capture (by 1 or both cameras) of the same individual at a unique station. Where animals were not identifiable by their features, one capture of that species at each station for that day constituted a capture (Chapter 5, Table 5.3).

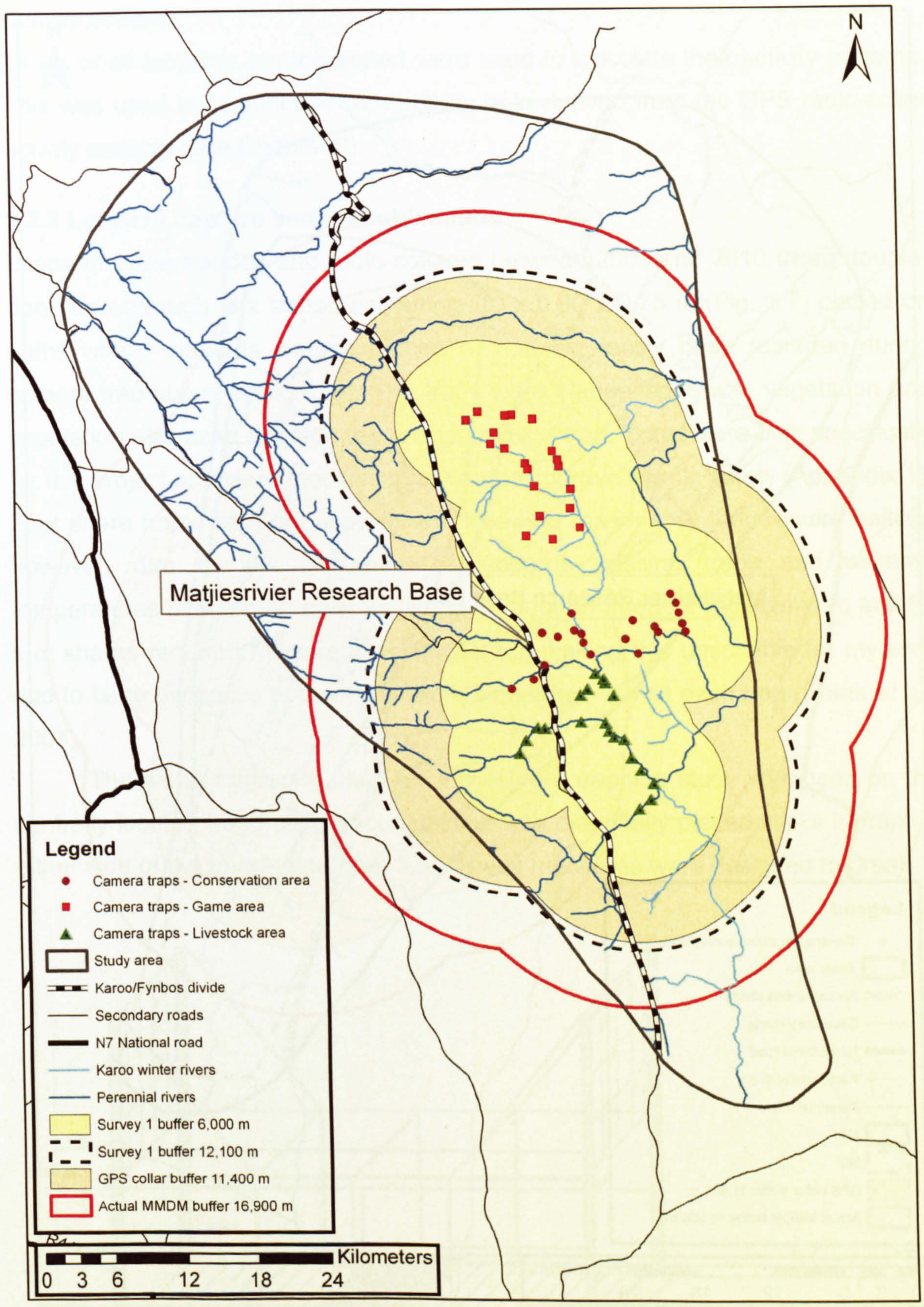


Figure 3.5. Cederberg camera trap surveys 1 and 2, where camtrap survey A was a livestock area, B a game area, and C a conservation area. Point buffers were calculated as 6000 m for MMDM; 12,100 m for FMMDM; 11,400 m for GPS home ranges and 16,900 m for 'GPS collar MMDM'.

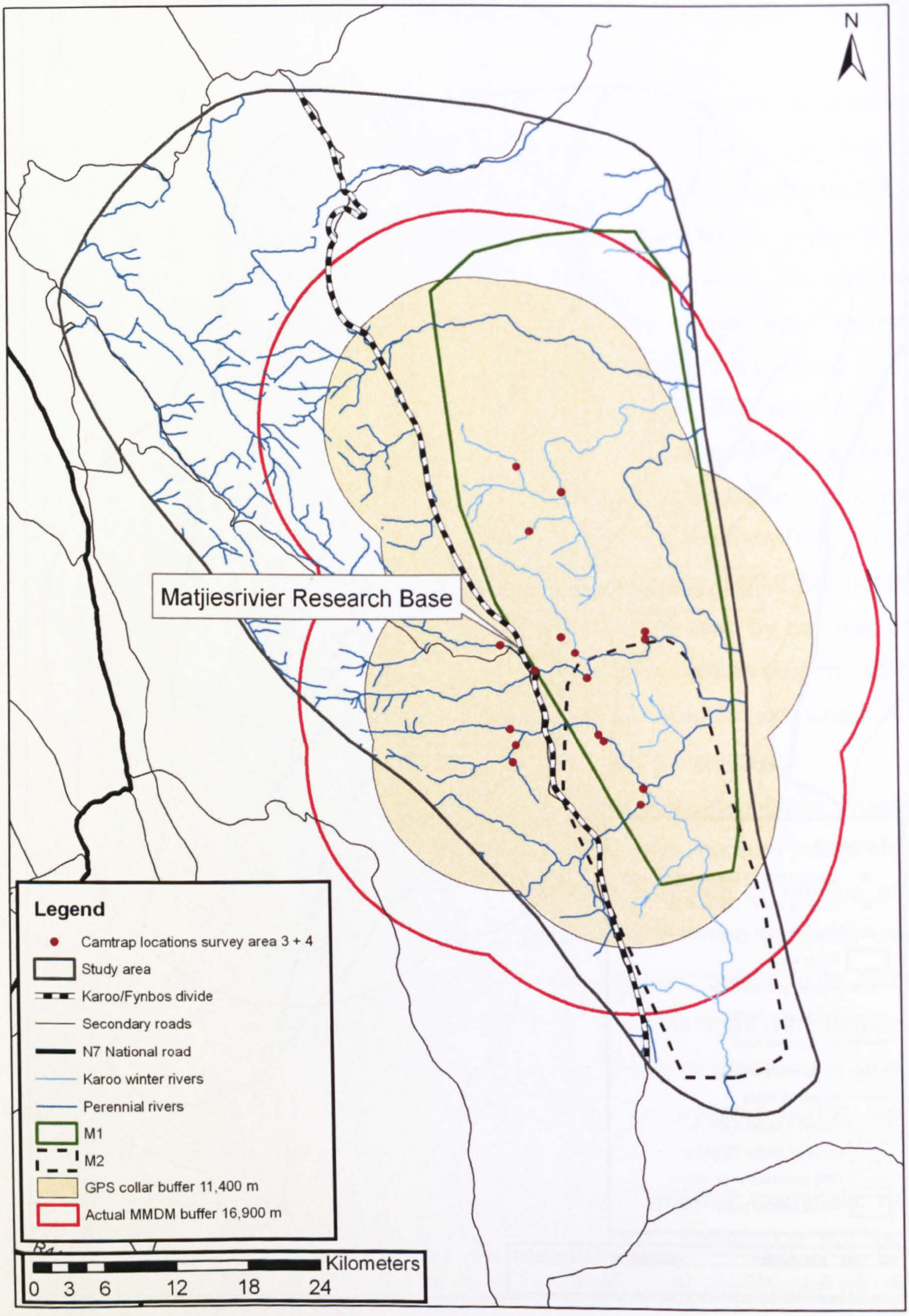


Figure 3.6. Cederberg camera trap surveys 3 and 4 with buffers. The 95% MCP home ranges for Karoo male leopards M1 and M2 are also shown.

Activity patterns

Times of all leopards photographed were used to calculate their activity patterns. This was used in conjunction with activity data derived from the GPS radio-collar activity sensors (see Chapter 6).

3.2.3 Leopard capture and immobilisation

Leopards were trapped and radio-collared between 2005 and 2010 using double-door walk-through box traps, measuring 2.0 x 0.80 x 0.75 m (Fig. 3.7) placed on paths where leopards were expected or had previously been recorded during camera trap surveys (Fig. 3.8). The traps were camouflaged with vegetation and vegetation was used to guide the animal into the trap. Traps were built specifically for this project and were modified over time to improve animal safety (Appendix 1). Foot snare traps were not used for the following reasons: (i) they require baiting, however, due to low frequency of leopards passing traps and extreme temperatures in summer, baits would have required frequent replacement; and (ii) foot snares required more regular monitoring, making this unsuitable for my area due to large distances and considerable time taken to visit each trap (Frank *et al.*, 2003).

The same fragrance used for the camera trapping study was used on the centrally located tread-plate in conjunction with diagonally placed sticks in front of either side of the tread-plate (Fig. 3.8). These measures were designed to break

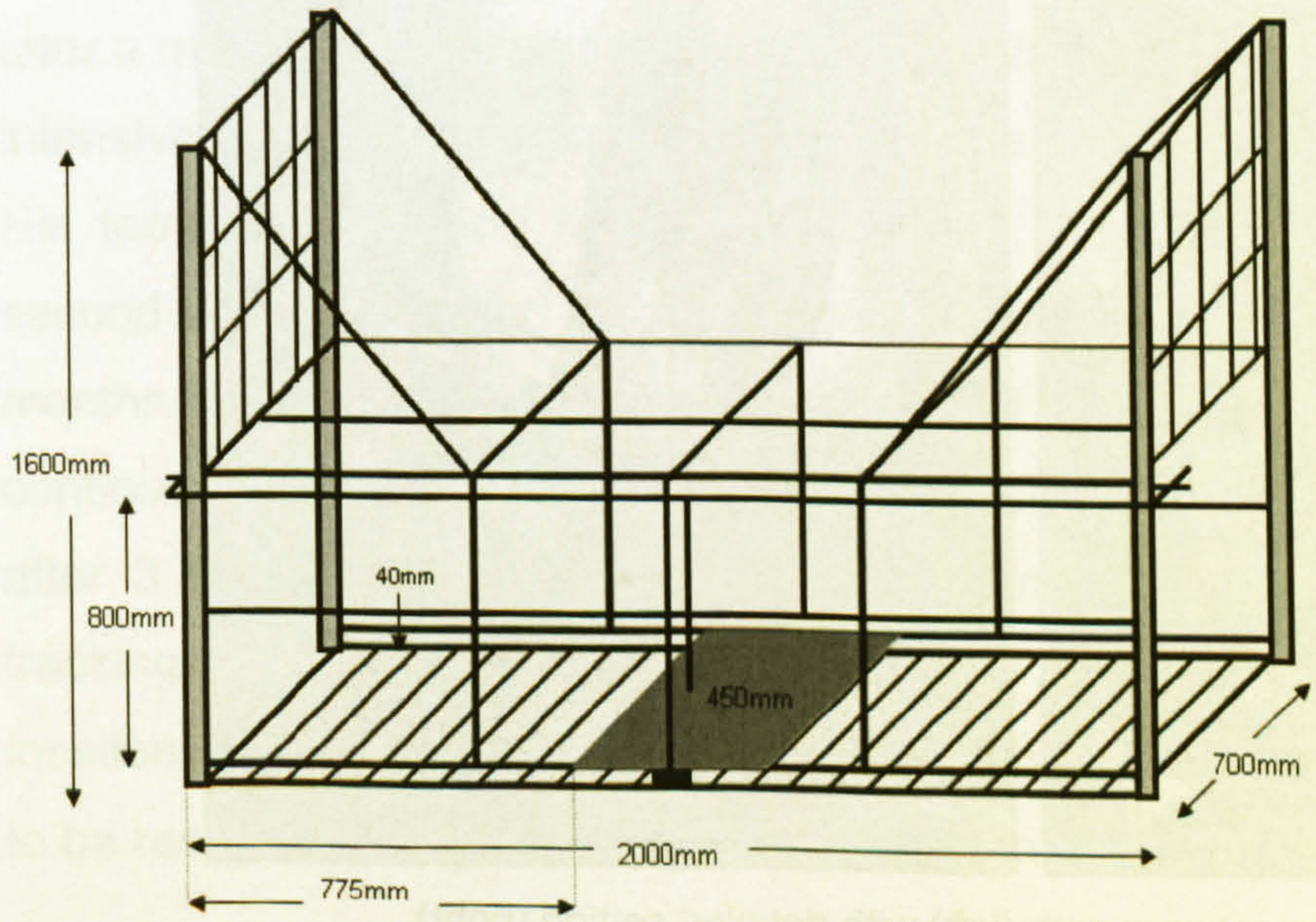


Figure 3.7. Double-door walk-through cage trap; the 50x50 mm soft, aluminium wire cover is not shown. The tread-plate was placed in the centre of the trap.

the momentum of the leopard and enhance the chance that it would place its foot on the tread-plate, thereby triggering the trap. Cage traps were monitored twice a day, once using a VHF trap transmitter that signalled when the doors dropped and once visually to look for signs of a leopard near the trap, as well for testing the transmitter. The trap transmitters (Telonics, Mesa, Arizona, USA) emitted a constant pulse, the frequency of which changed when the doors were down. Leopards were anesthetised by a veterinarian, initially using ketamine hydrochloride (Anaket-V, Bayer (Pty) Ltd., Isando, South Africa; dosage 10 mg/kg) mixed with xylazine hydrochloride (Chanazine, Bayer; (Pty) Ltd., Isando, RSA; dosage 1 mg/kg) and subsequently with teletamine-zolazepam (Zoletil® 100, Virbac, RSA (Pty) Ltd., Centurion, South Africa; dosage 5 mg/kg). Leopard weights were estimated visually by both the veterinarian and myself by approaching the cage for a brief inspection before moving off a suitable distance to load the tranquilizing dart with the correct drug dosage. Drugs were administered with a CO_2 dart pistol (DAN-INJECT ApS, Denmark) by resting the barrel of the pistol on the wire mesh, thereby ensuring a clear shot. A second person stood on the opposite end of the cage to distract the leopard, allowing for a well-placed dart in the thick-muscled rump of the animal.

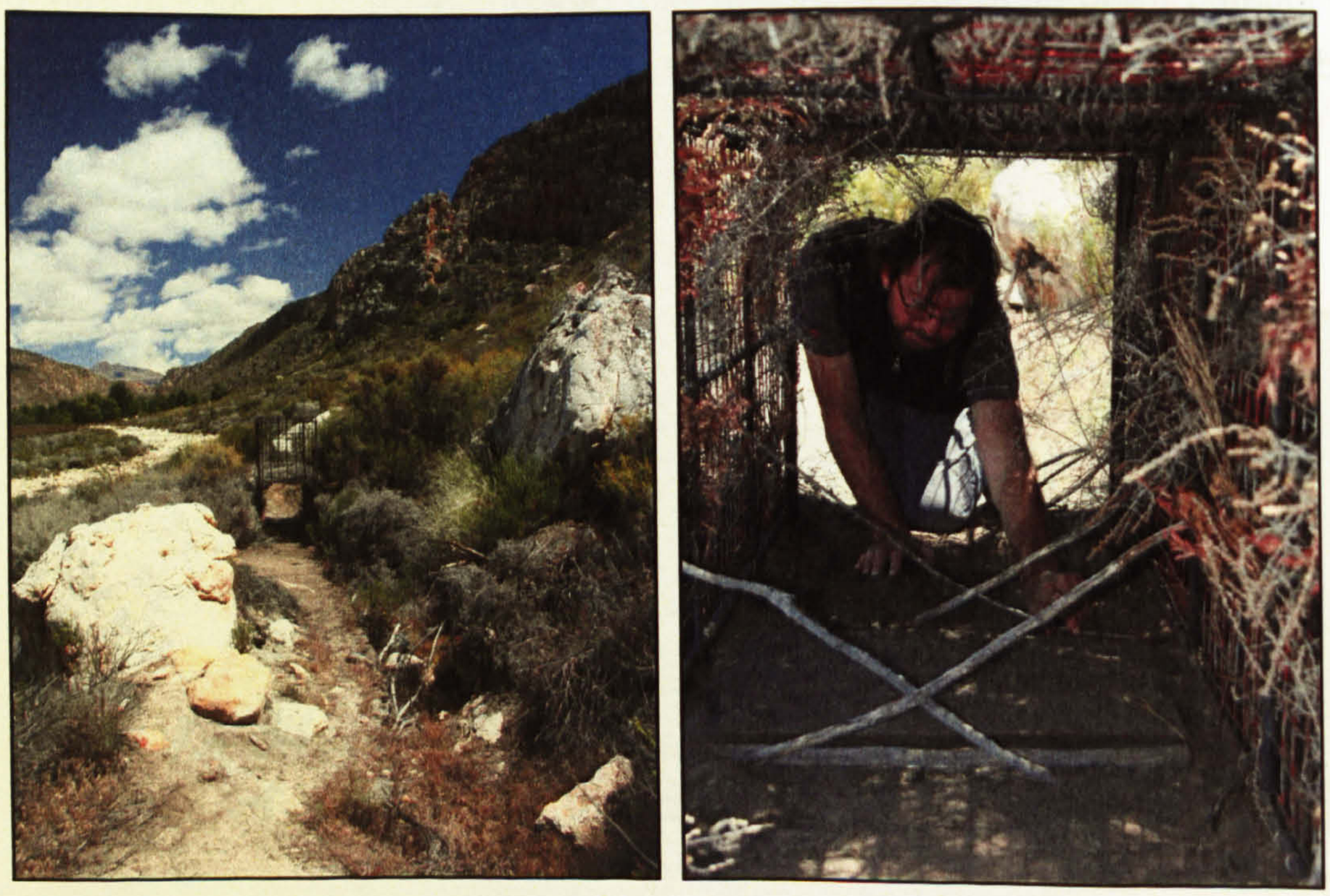


Figure 3.8. Leopard cage trap set on a path (left) with detailed setting (right).

Sedated leopards were examined for general health and breeding condition, weighed (± 0.5 kg), measured (± 1 cm), and aged by tooth colouration and wear (Stander, 1997). Anti-biotic ointment was administered to any visible injuries as well as the point where the dart had been embedded. Collared leopards were placed in a smaller holding cage and released once the effects of the anaesthetic had reduced sufficiently. Data were recorded on a capture sheet (Appendix 2). Table 3.4 summarises morphological data collected from trapped leopards, while Table 3.5 outlines the weights of leopards in different part of Africa. The average mass of adult male leopards in the Cederberg, was 35.0±2.5 kg (n=10), significantly larger than for females 20.5±1.5 kg (n=4) (Mann-Whitney *U* test: *U* =2, *n= 14,* P=0.008). Both male and female leopards in the Western Cape were significantly smaller than leopards recorded elsewhere in Africa (Mann-Whitney *U* test: Males: P=0.002; Females: 0.004).

Capturing and collaring conformed to Western Cape Provincial Government's and American Society of Mammalogists' (Gannon *et al.*, 2007) guidelines. Ethical approval was provided by CN. Where individuals were recaptured, I found no signs of collar abrasion on the neck (Fig. 3.9). Collars were removed on recapture of the animal. Male leopard M1 was collared twice, his first collar failing after 7 months. It took 7 months to recapture him, only to have his second collar fail after 2 months. I tried to recapture him to recover the collar but failed. M3 was collared twice, the first collar providing 6 months and the second collar 8 months of GPS location data. I was unable to retrieve the second collar after a mortality signal was detected in May 2007. Cage trapping efforts as well as intensive use of camera traps in the area resulted in no recaptures of this leopard. His territory was soon filled by male M11, who was also collared twice. The second collar was fitted without a gap in data collection, providing a total of 18 months tracking data. The same happened with M9, resulting in 14 months of continuous data. Female F5's collar worked poorly in this rugged environment, and after 3 flights with helicopter and fixed wing aircraft, as well as 8 months of tracking by vehicle and on foot, I was only able to download 3 months of GPS location data. Her collar had a remote drop-off unit which also failed. She has yet to be recaptured. Figure 3.10 provides the length of time leopards were monitored.

Figure 3.9. Photograph of the neck region of female F10 showing no signs of neck abrasion after being collared for 13 months.

3.2.4. GPS collars and data collection

VECTRONIC Aerospace GmbH (Berlin, Germany) GPS radio-collars and two Televilt Tellus (Televilt International, Lindesberg, Sweden) GPS collar, weighing <2% of an individual's body weight, were fitted to healthy adult leopards. All collars had UHF remote GPS downloading capabilities and were programmed to capture and store 4 - 24 GPS locations per day. Collar schedules relied on collar performance. I attempted to obtain uninterrupted data for a full year. Because leopards in this region were predominantly nocturnal (see Chapter 6), collars were principally programmed to capture 4 - 8 locations per day, with 3 - 5 of these being night-time locations (1800 - 0600) Central African Time. GPS data were downloaded by aircraft or on foot (from within 10 km) every 15.3±1.6 days where possible and plotted on 1:50,000 topographical maps using ArcGIS.

Table 3.4. Morphometric data of male (M) and female (F) leopards captured since 2004. Adult (A) is ≥3 years, sub-adult (SA) 1-3 years and juvenile (J) less than 1 year.

Unique ID	Date captured	Weight (kg)	Body Length (cm)	Head-tail (cm)	Tail length (cm)	Chest girth (cm)	Neck circ. (cm)	Head circ. (cm)	Head length (cm)
M1	23/02/2006	47	124	209	85	68	42	49	28
M2	17/07/2007	44	124	198	74	70	43	47	26
M3	13/08/2005	28	118	202	84	60	35	42	26
M6	23/08/2005	22	107	176	69	51	31	40	24
M7	17/07/2006	31	120	196	76	62	38	46	26
M8	20/10/2006	32	115	190	75	59	38	46	26
M9	13/11/2006	39	120	200	80	64	39	45	26
M10	01/05/2007	39	120	196	76	62	39	46	27
M11	11/11/2007	29	118	185	67	58	36	43	24
M14	02/11/2009	38	124	212	88	65	39	45	27
F10	18/06/2008	24	102	172	70	54	33	37	24
F5	14/07/2008	23	105	177	72	49	30	38	23
F6	31/01/2007	18	104	174	70	46	28	36	20
F9	01/09/2007	18	100	176	76	53	31	37	22
JM1	22/07/2007	19	95	158	63	46	29	35	21
SAM4	18/11/2004	25	96	162	66	52	33	42	24
SAM5	13/07/2005	25	108	179	71	52	30	38	24
SAF8	01/08/2006	18	92	156	64	43	27	35	22

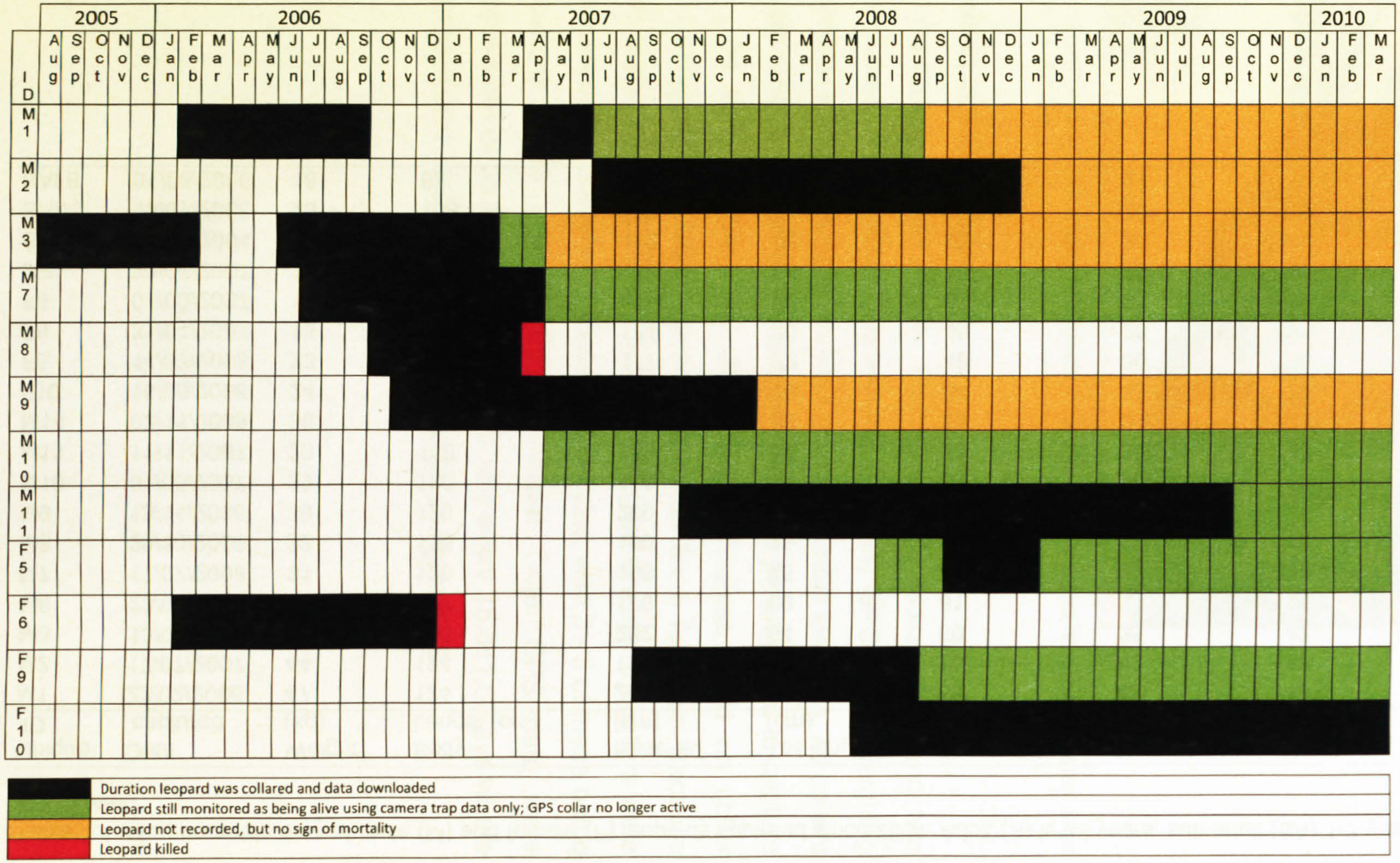


Figure 3.10. Time sheet with periods leopards were monitored in the Cederberg.

Table 3.5. Leopard mean weights derived from studies in Africa.

Study	Reference	Country	Habitat	Male (kg)	No.	Female (kg)	No.
1	Bailey, 1993	South Africa	Savanna	61	8	37	11
2	Balme, G., pers. comm. 22/09/2010	South Africa	Savanna	64	19	37	15
3	Grimbreek, 1992	South Africa	Mountain Savanna	59	5	35	6
4	Jenny & Zuberbühler, 2005	Ivory Coast	Forest	56	1	33	2
5	Norton & Lawson, 1985	South Africa	Mountain Fynbos	35	1	-	-
6	Marker & Dickman, 2005	Namibia	Savanna	46	6	32	4
7	Q. Martins, this study	South Africa	Mountain Fynbos and Karoo	36	6	21	4
8	Stuart, 1981	South Africa	Mountain Fynbos	31	27	21	9
9	Swanepoel, L., pers comm. 18/10/2010	South Africa	Mountain Savanna	60	6	40	6

CHAPTER 4

Home range and habitat use

Summary

The long-term conservation of far-ranging species requires good estimates of the size of the areas needed to support viable populations, the manner in which they inhabit these areas and what habitats are selected or avoided. I used GPS radio-collar data to determine the size of home ranges of leopards in the Cederberg Mountains, and to establish whether there were seasonal and/or sexual differences between the Karoo and Fynbos biomes. Three month's data proved sufficient to calculate asymptotic range sizes. I obtained GPS location data from 11 adult leopards (7 males, 4 females), whose 95% MCP home ranges varied from 74 – 910 km^2; male ranges were significantly larger than females ($P<0.04$). Home range overlap for males on a spatial and temporal basis was enough to suggest leopards inhabited exclusive ranges. Habitat selection analyses showed that leopards preferred rocky slopes near rivers and avoided open areas. I showed that Cederberg leopards have some of the largest ranges recorded for the species and that their selection of particular habitat types affected their range size, resulting in Karoo home ranges being larger than Fynbos ranges.

4.1. Introduction

A key part of assessing a species' vulnerability to population decline or extinction is to quantify the extent of its required habitat. This applies particularly to species with large ranges. Limited and/or fragmented habitats are a problem for species with large ranges, increasing their vulnerability to persecution (Woodroffe & Ginsberg, 1998). Where populations occur in conserved areas, such as reserves, core populations are protected, at least to some extent. However, boundaries to these areas, where species are not afforded protection, may act as population sinks, resulting in the decline or extirpation of the overall population (Balme *et al.*, 2010). In Chapter 5 I show that leopard densities in the Cederberg were low (0.6 – 2.3 leopards/100 km^2). Consequently, conserved areas would either be too small or shaped in such a way that leopard home ranges would inevitably overlap with privately owned land, often resulting in conflict with resident farmers due to

livestock losses. Hence one of my key aims was to obtain estimates of home range, habitat requirements and movement parameters to assist in the development of effective conservation management practices.

Utilising home range as a means to describe the way in which conspecifics arrange themselves within a given landscape provides insight into the processes which affect their survival. Burt (1943) defined a home range as "the area traversed by the individual in its normal activities of food gathering, mating and caring for young", and excludes the "occasional sallies" from home range calculations. In calculating home range, MCPs (Mohr, 1947) have several disadvantages (Harris *et al.*, 1990). For instance, this 'conceptual' method does not consider any area beyond the boundaries of the polygon fitted to the outer locations (Powell, 2000), thereby suggesting that the animal has no knowledge of the area beyond its home range. Nor does it provide any measure of internal space use (Worton, 1987). However, MCPs have the advantage that they are comparable with most studies (Harris *et al.*, 1990) and provide information showing the space required to support members of the species (Burt, 1943). Considering the variation in home range size reported in leopard studies elsewhere (Hamilton, 1976; Norton & Lawson, 1985; Norton & Henley, 1987; Bailey, 1993; Stander & Hayden, 1997; Mizutani & Jewell, 1998; Marker & Dickman, 2005), population-specific data are needed to quantify how leopards adapt to local conditions.

Leopards live in extremely varied habitats, where patterns of habitat selection should have a significant effect on resulting home range sizes, depending on resource preferences or the availability of suitable habitats within their range, i.e. habitat used vs available (Aebischer *et al.*, 1993). These patterns are fundamental to understanding leopard ecology (Marker & Dickman, 2005), and may depend on a carnivore's energy constraints, body mass, habitat type, vegetation cover, topography, human presence, prey availability and abundance (Gittleman & Harvey, 1982; Jackson, 1996; Benson *et al.*, 2006). Grid analysis provides a useful means to determine habitat usage (Harris *et al.*, 1990; Mizutani & Jewell, 1998), while gender is commonly a factor determining home range size. Female home range size is expected to be determined by food availability (Sandell, 1989). Male leopard home ranges may be expected to be larger than

females due to their larger body size and greater metabolic needs. The polygamous mating system of leopards generally results in home range size being determined by distribution of females (Sandell, 1989).

In this chapter, I examined the social and spatial organisation of leopards in two diverse biomes in the Cederberg Mountains. Specifically my aims were to: (i) determine leopard home range sizes and home range overlap between individuals on a spatial and temporal basis; (ii) examine leopard habitat use in both the Karoo and Fynbos biomes, identifying features influencing their movement patterns; and (iii) compare observed versus expected home ranges based on the metabolic requirements of male and female leopards in the Karoo and Fynbos biomes.

4.2. Methods

4.2.1. Study area

See Chapter 2.

4.2.2. Leopard capture and immobilisation

See Chapter 3.

4.2.3. Home range analysis

Leopard home ranges using MCP and Fixed Kernel (FK) methods were determined using ArcGIS 9.2. I used all GPS location data when examining 95% and 100% MCPs. FKs (60% and 95%) were calculated using HRT: Home Range Tools for ArcGIS Version 1.1 (Rodgers *et al.*, 2007). Data were analysed separately for animals collared more than once, but separated in time. Individual smoothing factors were determined by starting with a smoothing parameter which displayed 'broken' polygons. The h_ref was then adjusted until a single polygon was generated (A. Rogers, pers. comm., 19/06/2010). GPS locations for FKs were separated by *c.* 24 hrs (Swihart & Slade, 1985) and tested for signs of auto-correlation using the HRT tool. Using the program Ranges 6 (Kenward *et al.*, 2003), I plotted the number of GPS locations incrementally against home range size, as well as percentage home range used (100% MCP), to establish whether an animal's range showed signs of reaching an asymptote (Harris *et al.*, 1990). Differences between sexes and seasons were also investigated. Seasonal

calculations were conducted using 95% MCPs for all data over 3 months (see Results on asymptotal data). Where an individual was collared for a considerable period and had 2 or more of the same season's data, these data were averaged.

Home range overlap and dynamic interaction analyses were performed with 95% MCPs using Ranges 6. Analyses were performed for static interactions, where ranges were analysed on a spatial level only; for dynamic interactions, data from neighbouring or overlapping animals were used when corresponding locations were within 30 min of each other (Macdonald *et al.*, 1980; Kenward *et al.*, 1993). A Jacobs' Index (Jacobs, 1974) generated from the dynamic interaction analyses indicated whether individuals were (i) avoiding each other (closer to -1), (ii) attracted to each other (closer to +1) or (iii) displayed no signs of either behaviour (closer to 0).

Metabolic home ranges of males determined by female energy requirements were calculated using the equation:

$$R_{male} = R_{female} \times (M_{male}^{0.75} / M_{female}^{0.75})$$

where R is the metabolic home range and M the average body mass (Mizutani & Jewell, 1998).

Female F10 was the only female to be monitored with cubs during my study. Data were captured for 3 months after she produced two cubs, which restricted her movements. So data for these three months were analysed separately using 60% FK and 95% MCP to avoid a distortion of her home ranges and behaviour.

4.2.4. Grid-cell analysis

I used grid-cell analysis to compare habitat use between the two different biomes (Fig. 4.1). The percentage of available habitat used was determined by: (i) producing a 95% MCP using 180 successive 1-day GPS locations for each leopard, where these were plotted on grid-cells falling within or touching the 95% polygon, and where the grid size was calculated as half the median of the distance between successive points for all leopards (L. Underhill, pers. comm., 17/06/2010); (ii) counting the total number of grid cells as well as the number of grid cells populated by GPS points; empty cells surrounded on 3 or 4 sides by

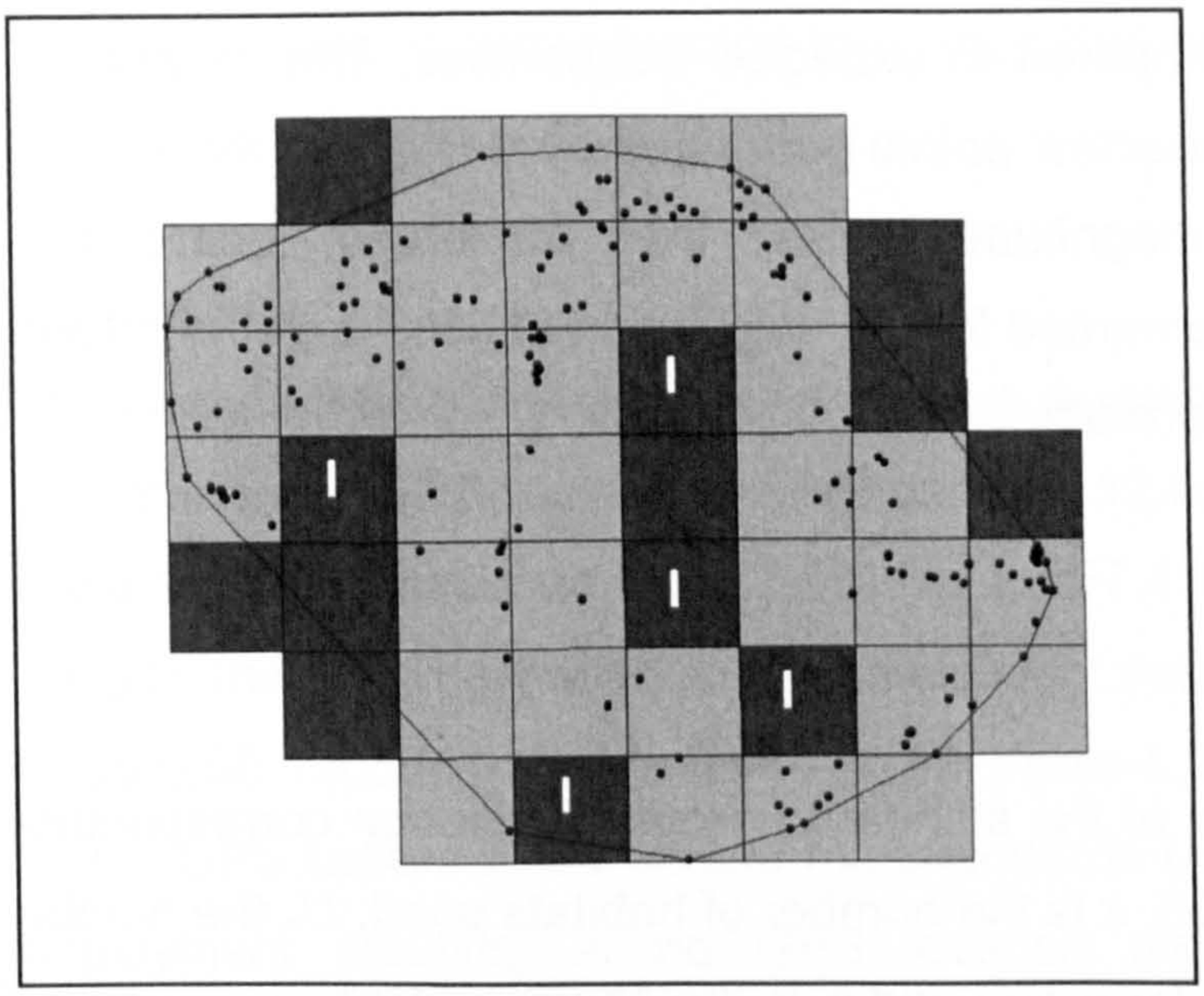


Figure 4.1. Grid-cells of female leopard F6, where each point is 1 GPS location per day for a 180 day period. The outer polygon denotes the 95% MCP. Each grid-cell is 1.5 km x 1.5 km, where the total number of grids = grids within and touching the 95% MCP polygon. Cells containing a GPS point were 'occupied' cells, while cells labelled 'I' were included in the total because they were surrounded on 3 or 4 sides by occupied cells.

populated cells were included as occupied cells; and (iii) the percentage of occupied vs empty cells was calculated to compare the percentage use between habitats. The 180 days were chosen randomly and do not reflect seasons because there was no seasonal difference in range sizes and leopards with less than 180 days data were excluded from these analyses.

4.2.5. Habitat use of leopards

I used all GPS radio-collar data at a home range level to formulate resource selection indices; this is a robust means of measuring habitat selection (Manly *et al.*, 2002). Habitat availability was delineated by 95% MCP home ranges of overlapping or adjoining leopards (Broomhall *et al.*, 2003). Contiguous ranges were joined together to form one polygon; habitat proportions are shown in Table 4.1. The proportion of habitat present was derived by calculating the total for each habitat type within each leopard's 95% MCP range.

Habitat variables were mapped using ArcGIS 9.2; variables included habitat type, distance to rivers, slope and elevation at a 30 m pixel resolution (SPOT5 Tiles 2007, CSIR Satellite Application Centre). GPS locations were allotted a figure corresponding to the value or class given to each habitat attribute, and

observed frequencies were compared to expected frequencies. The distance-to-river class required random 'expected' points generated by Hawth's tools (ArcGIS) (Beyer, 2004) an order of magnitude greater than 'observed' locations. A Bonferroni correction was implemented for the calculation of 95% upper and lower confidence intervals using the formula:

$$Z_{\alpha/2k}\sqrt{[o_i\,(1-o_i)/(U_+\pi_i^2)]}$$

where: $Z_{\alpha/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area $\alpha/2k$, α=0.05, k is the number of habitats used, U_+ the number of used locations for that particular group and o_i is the observed frequency used. If use was proportional to availability (random use), the lower and upper confidence interval (C.I.) overlaps with 1. When use is greater than availability the ratio is >1 and implies selection; a ratio of <1 implies avoidance (Manly *et al.*, 2002). For comparison, selection and avoidance of habitats was also measured using Jacobs' indices. Using Jacobs' indices where positive values tending to 1 showed

Table 4.1. Habitat proportions for the Karoo and Fynbos biomes in the Cederberg study area.

	Karoo vs Fynbos		
	All areas (%)	Karoo (%)	Fynbos (%)
Habitat type			
Human habitat	1	0	2
Open plain	32	46	6
Rocky slope	35	18	66
Smooth slope	12	14	8
Rocky flat	19	21	17
Distance to rivers			
<50 m	16	14	19
50<150 m	28	25	33
150<1600 m	56	61	47
Elevation			
<500 m	14	14	14
501 - 800 m	35	42	35
801 - 1200 m	39	42	39
1201 - 1600 m	11	2	11
1601 - 2000 m	1	0	1
Slope			
<5 degrees	28	33	18
5<15 degrees	41	42	40
15<25 degrees	18	16	22
25<35 degrees	9	7	12
>35 degrees	4	3	7

selection, whereas those tending to -1 indicated avoidance (Jacobs, 1974; Manly *et al.*, 2002; McCarthy *et al.*, 2005).

4.3. Results

Thirteen adult leopards were collared from August 2005 till March 2010 providing 129 months of GPS tracking data (mean±SE 12.0±1.5 months). Collar success at retrieving GPS locations was 75.8% (range 57.4% - 87.6%) of the total locations programmed for download and cumulatively resulted in 20,952 GPS locations (mean±SE 1905±414, range 358 – 4785; Table 4.2).

GPS collars failed on two male leopards (M10 and M14) immediately after deployment resulting in no GPS location data. Of eleven leopards which successfully provided GPS data, four (2 males, 2 females) were tracked in the Karoo, seven (5 males; 2 females) in the Fynbos.

4.3.1. Home range analysis

Incremental area curves using 100% MCP indicated variable rates of home range stabilisation (Fig. 4.2). Home range asymptote was clearly reached for at least 8 of the 11 leopards; M7, M9 and F5 showed no signs of reaching an asymptote. Leopards with non-asymptotic ranges had shifting home ranges, meaning that they had similar home range requirements to other leopards despite an asymptote not being reached. M9, for example, showed initial signs of home range stabilisation after *c.* 3 months (Fig. 4.2). The death of M8 in March 2007, resulted in M9 incorporating 59% of M8's home range into his, resulting in a dramatic increase in his home range from 66 – 132 km^2 (Fig. 4.3). M11's range appeared to shift after 1 year of tracking. However, M6 had simultaneously moved into the southern part of M11's range, possibly forcing the range shift. Only 3.5 months of data were available for F5. Earlier camera trapping records indicated that she had shifted her range to occupy the vacant territory remaining after F6's death in December 2007.

M1's range increased dramatically from collar 1 to collar 2 (there was a 7 month gap between the two collars). The sudden increase in range size by M1 of 415 km^2 suggested the neighbouring male leopard's territory had been taken over

by M1. M2's home range also similarly showed a sudden increase in home range size (Fig. 4.2), most likely related to his range shift into M1's range following the range shift of M1. Dramatic increases in home ranges were also noted during mating forays by females. For example, F6 accompanied M2 for 4 days (21 – 25

Table 4.2. Number of GPS locations and collar success for leopards in the Cederberg.

Leopard.	Sex	Biome	First collared	Collar success (%)**	No. of locations
M1*	Male	Karoo	23/02/2006	60.4	1142
M2	Male	Karoo	17/07/2007	87.6	2650
M3*	Male	Fynbos	13/08/2005	63.2	2097
M7	Male	Fynbos	17/07/2006	57.4	1001
M8	Male	Fynbos	20/10/2006	86.5	836
M9	Male	Fynbos	13/11/2006	86.3	2196
M10	Male	Fynbos	01/05/2007	-	-
M11*	Male	Fynbos	11/11/2007	83.3	3775
M14	Male	Fynbos	02/11/2009	-	-
F5	Female	Karoo	18/06/2008	-	358
F6	Female	Karoo	31/01/2007	72.4	1087
F9	Female	Fynbos	01/09/2007	74.1	1025
F10*	Female	Fynbos	14/07/2008	87.0	4785

* Leopard captured and collared more than once

** Collar success was the percentage of locations obtained from a programmed collar GPS schedule

Table 4.3. Home ranges, habitats and period tracked using GPS radio-collars for 11 collared leopards in the Cederberg Mountains between 2004 and 2010 using 95% and 100% Minimum Convex Polygons (MCP) with all locations, and Fixed Kernels (FK) using 1 location per day (60% and 95%). All home range figures are given in km^2.

ID	Habitat	Months	MCP 95	MCP 100	FK 60	FK 95	95 MCP	
							Summer	Winter
M1	Karoo	9	910	1190	374	1240	-	516
M2	Karoo	17	428	481	168	486	347	409
M3	Fynbos	14	216	317	98	264	176	198
M7	Fynbos	9	140	162	58	164	63	136
M8	Fynbos	5	100	114	38	118	100	-
M9	Fynbos	14	132	232	63	164	107	125
M11	Fynbos	18	264	322	112	290	165	146
F5	Karoo	3	203	249	107	345	203	-
F6	Karoo	11	100	302	60	155	98	99
F9	Fynbos	11	74	116	38	99	65	74
F10*	Fynbos	18	89	180	30	88	62	61
F10**	Fynbos	3	37	51	9	37	37	-

* F10 before having cubs

** F10 for 3 months after producing a litter of 2 cubs

September 2007), moving considerably beyond her 'normal' range. The mating foray resulted in an increase in her 100% MCP range from 100 - 302 km^2. A mating foray was also displayed by F10, who increased her range while mating with M6.

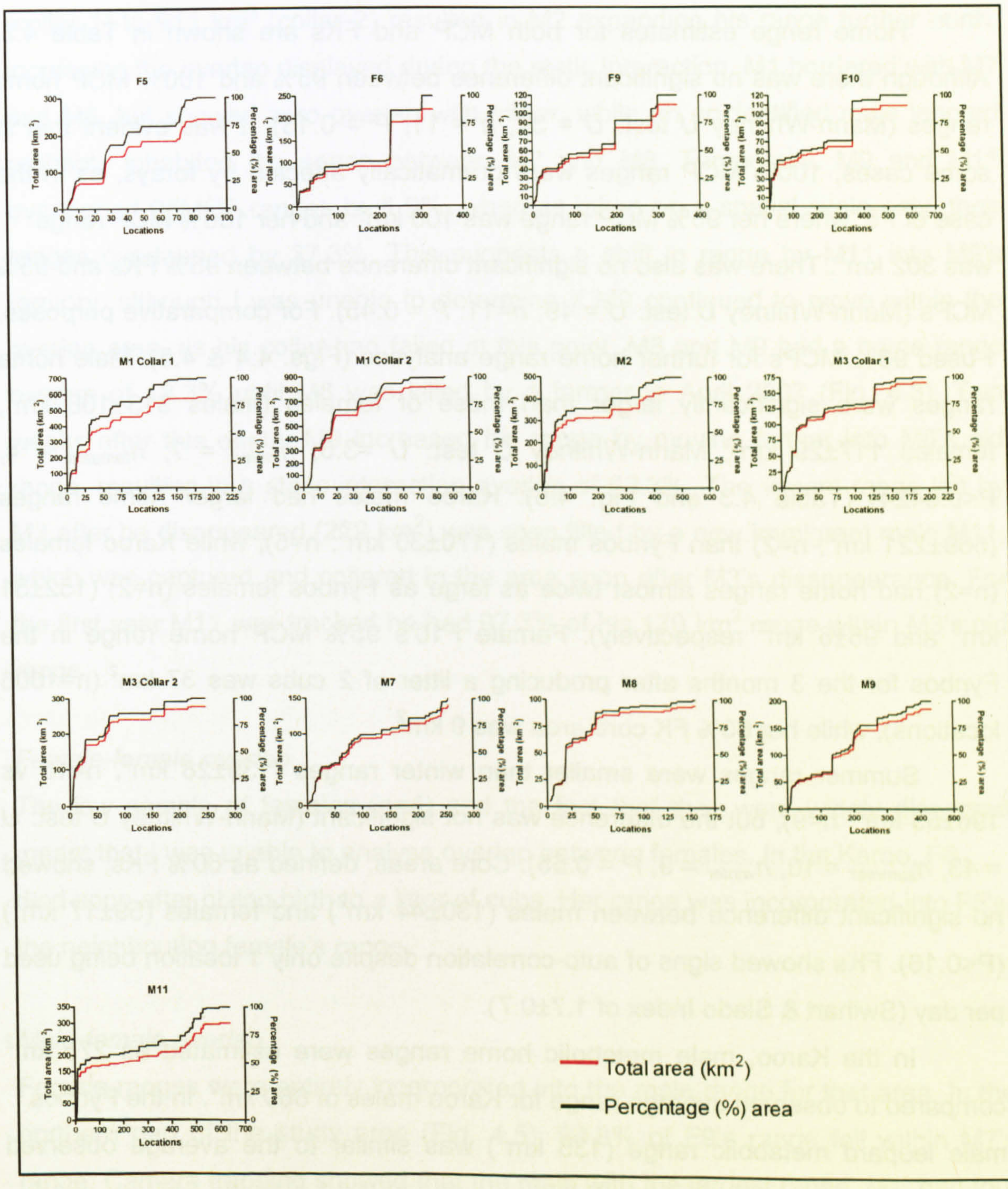


Figure 4.2. Incremental area curves as determined by 100% MCP home range estimates for 11 leopards using 1 location per day. M1 and M3 were each collared twice with several months between captures. M7, M9 and F5 appeared not to reach an asymptote.

4.3.2. Home range size

The home ranges of 11 leopards were determined using 95% and 100% MCPs for both 1 location per day as well as all location data. Home ranges for the two methods did not differ significantly (Mann-Whitney *U* test: *U* =54, *n=11*, P=0.55) and so all locations were used for further analyses.

Home range estimates for both MCP and FKs are shown in Table 4.3. Although there was no significant difference between 95% and 100% MCP home ranges (Mann-Whitney *U* test: *U* = 37, *n* = 11, *P* = 0.13), it was evident that in some cases, 100% MCP ranges were dramatically affected by forays, as in the case of F6, where her 95% MCP range was 100 km^2 and her 100% MCP range was 302 km^2. There was also no significant difference between 95% FKs and 95% MCPs (Mann-Whitney *U* test: *U* = 49, *n*=11, *P* = 0.45). For comparative purposes, I used 95% MCPs for further home range analyses (Figs. 4.4 & 4.5). Male home ranges were significantly larger than those of females (males 313±108 km^2, females 117±29 km^2; Mann-Whitney *U* test: *U* =3.5, n_{males} = 7, $n_{females}$ = 4, P<0.0424) (Table 4.3 and Fig. 4.5). Karoo males had larger home ranges (669±221 km^2; n=2) than Fynbos males (170±30 km^2; n=5), while Karoo females (n=2) had home ranges almost twice as large as Fynbos females (n=2) (152±51 km^2 and 95±6 km^2 respectively). Female F10's 95% MCP home range in the Fynbos for the 3 months after producing a litter of 2 cubs was 37 km^2 (n=1006 locations), while her 60% FK core area was 9 km^2.

Summer ranges were smaller than winter ranges (139±28 km^2, n=10 vs 196±53 km^2, n=9), but the difference was not significant (Mann-Whitney *U* test: *U* = 43, n_{summer} = 10, n_{winter} = 9, *P* = 0.55). Core areas, defined as 60% FKs, showed no significant difference between males (130±44 km^2) and females (59±17 km^2) (P<0.16). FKs showed signs of auto-correlation despite only 1 location being used per day (Swihart & Slade Index of 1.7±0.7).

In the Karoo, male metabolic home ranges were estimated as 275 km^2 compared to observed average range for Karoo males of 669 km^2. In the Fynbos male leopard metabolic range (135 km^2) was similar to the average observed range (170 km^2).

4.3.3. Home range overlap

Male-male overlap

Bordering males (95% MCP) had an average static home range overlap of 27.4±12.2% (n=5). Range overlap was affected if temporal considerations were not taken into account. Karoo male M1's dramatic range expansion from 465 km^2 (collar 1) to 911 km^2 (collar 2) resulted in M2 expanding his range further north, increasing the overlap displayed during the static interaction. M1 bordered with M7 and M3, but showed zero overlap with either, while an unidentified male leopard probably inhabited the space between M7 and M8. Temporally, M9 and M11 overlapped 95MCP ranges by 1.9%, whereas taken on a spatial scale only, their ranges overlapped by 37.3%. This suggests a shift in range by M11 into M9's territory, although I was unable to determine if M9 continued to move within the overlap area, as his collar had failed at this point. M8 and M9 had a home range overlap of 18.3% until M8 was killed by a farmer in April 2007 (Fig. 4.3). Two weeks after this death, M9 increased his range by moving further into M8's old range, resulting in a static interaction overlap of 63.3%. The vacant range left by M3 after he disappeared (229 km^2) was soon filled by a new immigrant male M11, which was captured and collared in the area soon after M3's disappearance. For the first year M11 was tracked he had 97.3% of his 179 km^2 range within M3's old range.

Female-female overlap

The low sample of females (n=4) and the fact that they were widely dispersed meant that I was unable to analyse overlap between females. In the Karoo, F6 died soon after giving birth to a litter of cubs. Her range was incorporated into F5's, the neighbouring female's range.

Male-female overlap

Female ranges were entirely incorporated into the male range for that area. In the northern part of the study area (Fig. 4.5), 94.8% of F9's range fell within M7's range. Camera trapping showed that the male with the largest range, M1, had four females (F2, F3, F5 and F6) within his range. M1 maintained the largest range of all males.

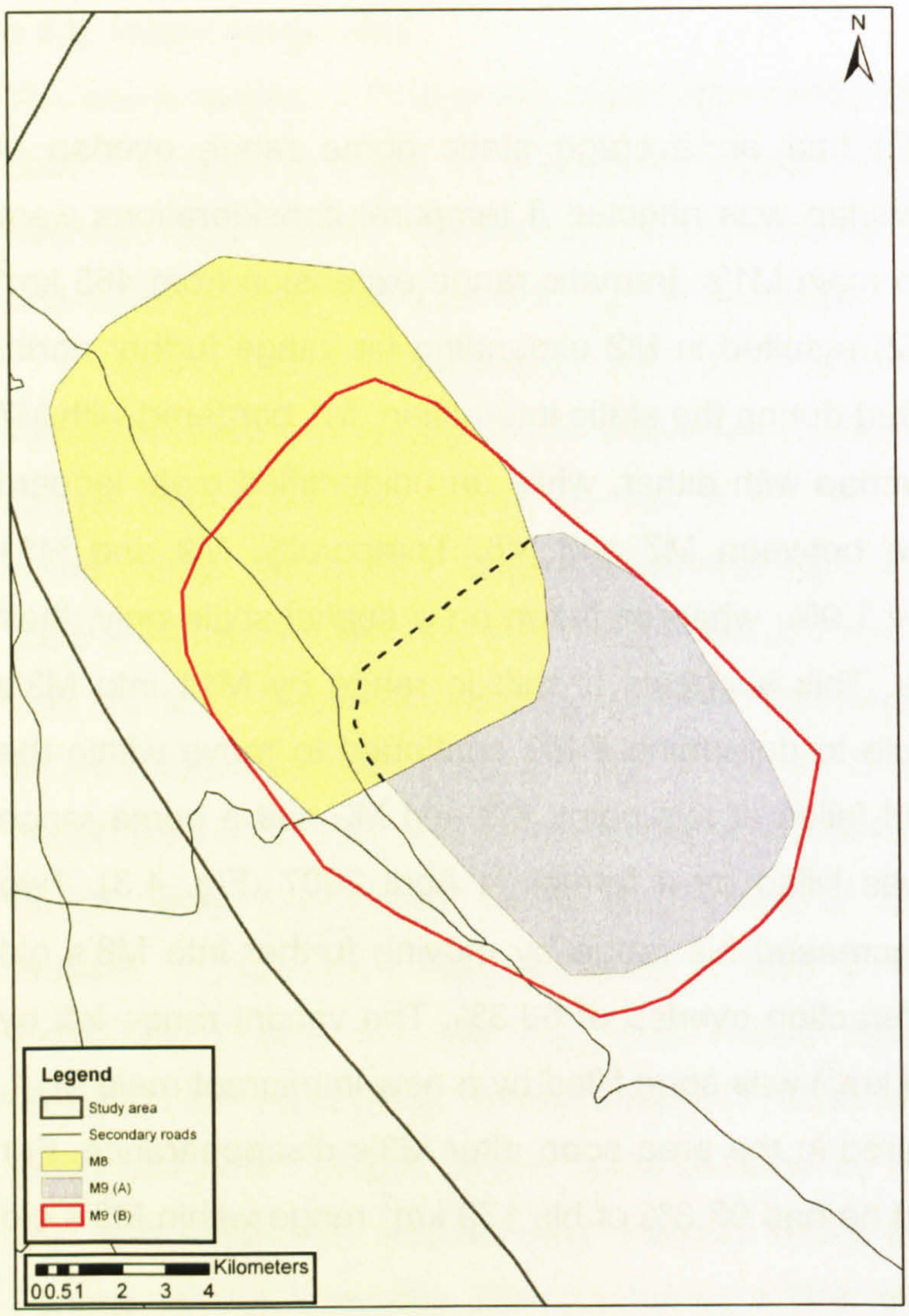


Figure 4.3. Overlapping range of M9 with M8 before (A) and after (B) M8's death in the Cederberg Mountains; all ranges are 95% MCPs.

4.3.4. Leopard dynamic interaction

Dynamic interactions between leopards collared at the same time and with overlapping ranges were determined for leopards M8 and M9, M1 and F6, and M11 and F10. Jacobs' Index values for all 3 were close to 0 (0.04±0.02), suggesting no significant interaction between individuals.

4.3.5. Percentage habitat use

Half the median distance moved between fixes for all leopards was 1.5 km, and so grid cells of 1.5 x 1.5 km (2.25 km^2) were used. Two leopards, F5 and M8, were excluded from grid-cell analyses due to insufficient data. The average number of grids forming a 95% MCP for a leopard in the Karoo was 154±60, 61±6 for the

Table 4.4. Habitat use for 9 leopards in the Cederberg Mountains. Each grid cell was 2.25 km^2 (1.5 x 1.5 km), while available grids were incorporated in a 95% MCP for each leopard. The number of grids cells used was calculated from 180 1-day points for each leopard; see text for details.

ID	Habitat	Grids used	Grids available	Percentage used (%)
M1	Karoo	117	255	46
M2	Karoo	87	161	54
M3	Fynbos	55	85	65
M7	Fynbos	56	66	85
M9	Fynbos	41	48	85
M11	Fynbos	57	74	77
F6	Karoo	38	47	81
F9	Fynbos	40	44	91
F10	Fynbos	39	50	78

Fynbos. On average male and female Karoo leopards used 61±11% of their available habitat, whereas those in the Fynbos used 80±4% (Table 4.4).

4.3.6. Habitat selection in the Cederberg

Both selection indices and Jacobs' indices suggest significant selection for rocky slope habitat in the Karoo and Fynbos; rocky slope only formed 18% of the available habitat in the Karoo, 66% in the Fynbos. In contrast open and flat habitats, 46% of the available habitats in the Karoo, were significantly avoided (Table 4.3). Leopard movement within human habitat was minimal, barring exceptional circumstances such as when F10 spent a considerable time feeding on domestic livestock (geese, chickens and one goat kid) near the farm Driehoek in winter 2009. This accounted for 57% of all the time leopards spent within human habitat.

Leopards selected proximity to rivers, especially within 50 m. The distance to river class 50<150 m indicated selection for slopes of both perennial and non-perennial rivers. Distances >150 m from rivers were significantly avoided. Elevations of 1201 - 1600 m were selected by all leopards, but lower elevations were selected in the Karoo: here the <500 m class was selected even though it only formed 14% of the Karoo habitat, while the class 801 - 1200 m (42% of available habitat) was avoided. Slopes <15 degrees were generally avoided in all habitats by males and females. The slopes used most significantly were between 15<35 degrees, while no preference was shown for steep slopes >35 degrees.

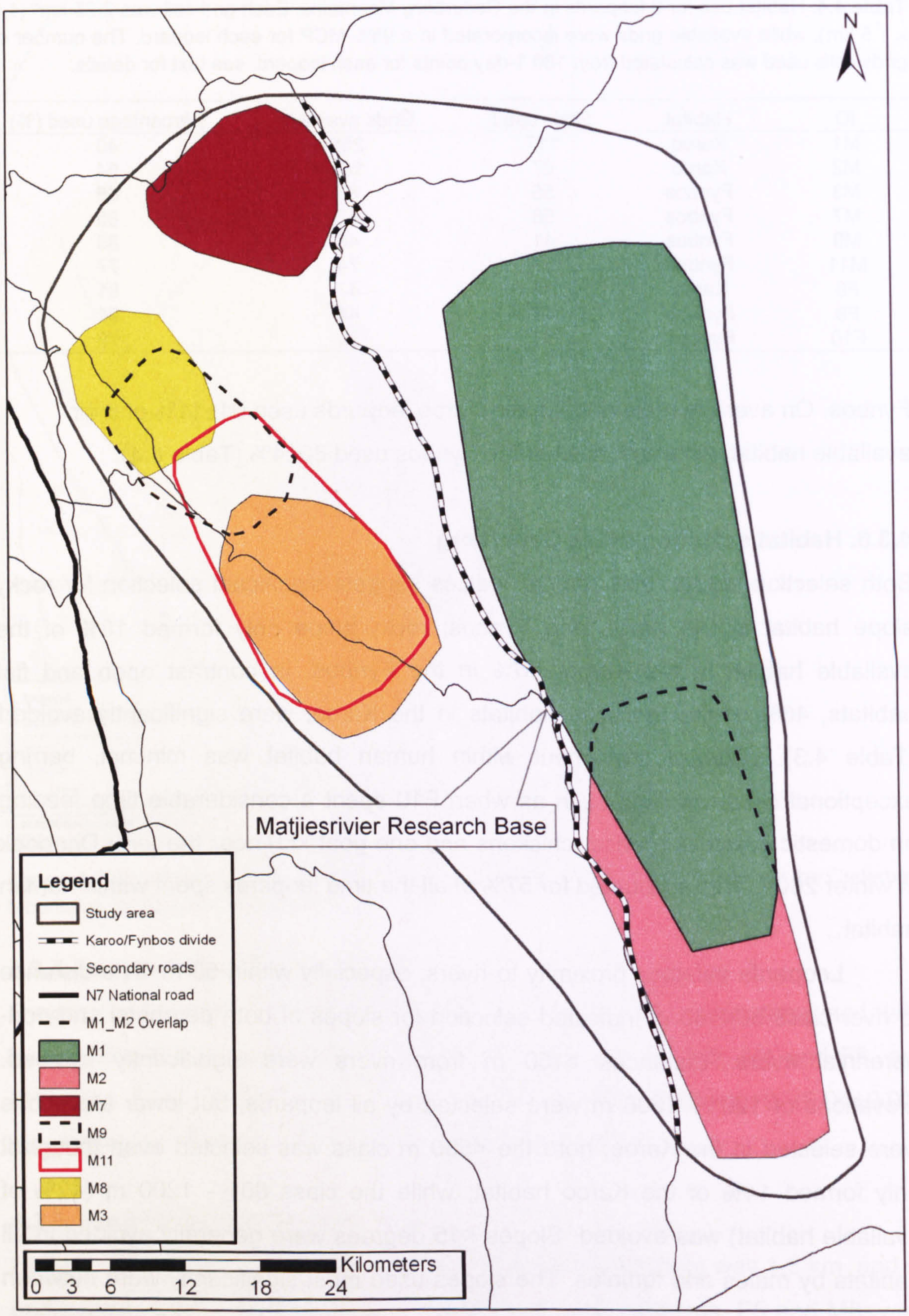


Figure 4.4. 95% MCPs for 7 male leopards in the Cederberg Mountains.

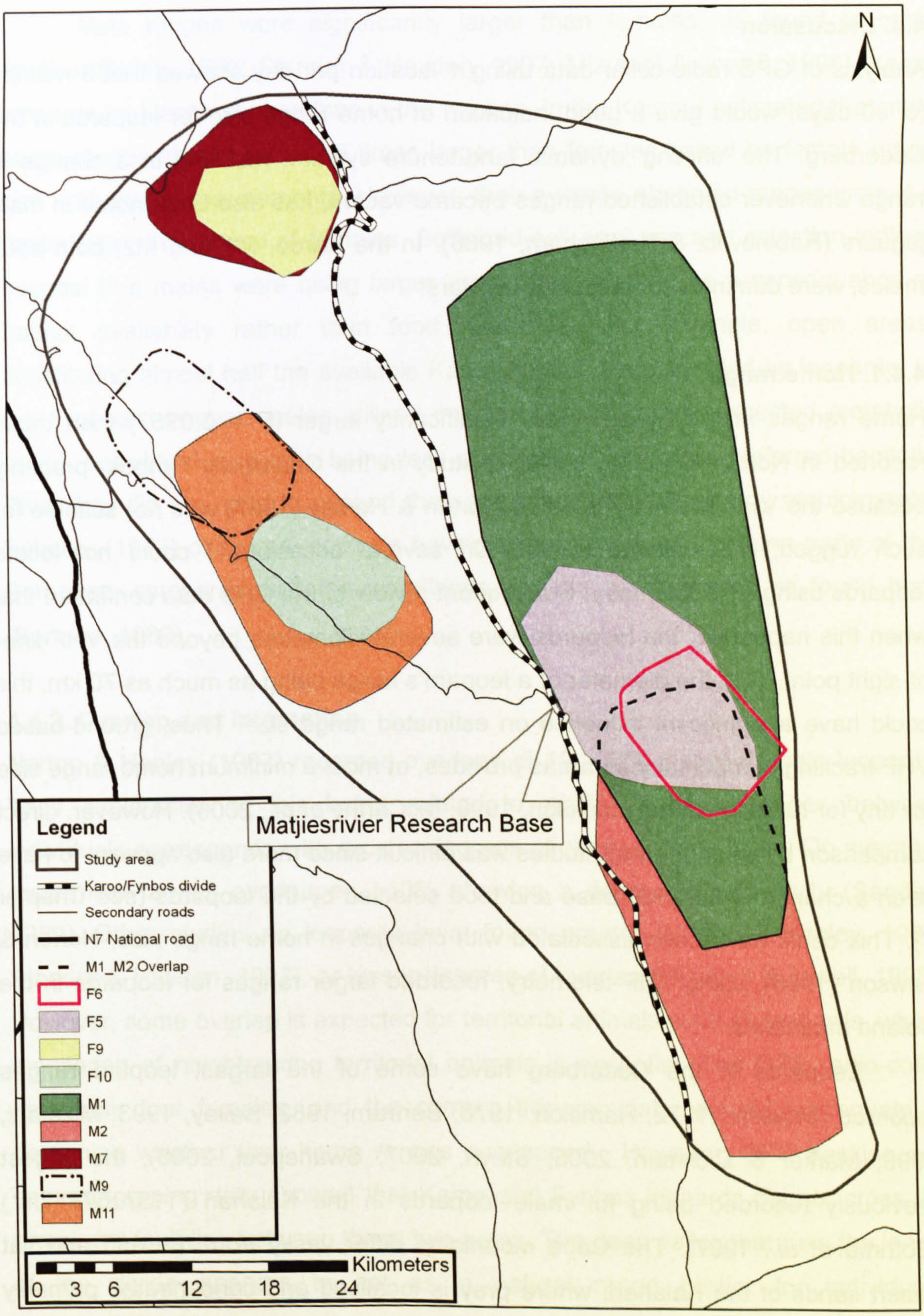


Figure 4.5. 95% MCPs for 4 female leopards, showing their spatial organisation with respect to 5 males in the Cederberg Mountains.

4.4. Discussion

Analysis of GPS radio-collar data using 1 location per day showed that 3 months (*c.* 90 days) would give a good indication of home range size for leopards in the Cederberg. The 'shifting' dynamic land-tenure system, resulting in a change in range whenever established ranges became vacant, has also been noted in male jaguars (Rabinowitz & Nottingham, 1986). In the Karoo, M1 and M2, both adult males, were dominant for at least four years.

4.4.1. Home range

Home ranges in the Fynbos were significantly larger ($P = 0.0357$) than those reported in Norton & Henley's (1987) study in the Cederberg Fynbos, probably because the VHF telemetry used by Norton & Henley (1987) was not suitable for such rugged, mountainous terrain. On several occasions I could not locate leopards using VHF telemetry. Subsequent review of the GPS data confirmed that when this happened, the leopards were several kilometres beyond the VHF line-of-sight point. With the diameter of a leopard's range being as much as 70 km, this could have a significant influence on estimated range size. Thus, ground-based VHF tracking in mountainous areas provides, at most a minimum home range size for any far-ranging animal (Jackson, 1996; McCarthy *et al.*, 2005). However, direct comparison between the two studies was difficult since there also appears to have been a change in the prey base and food selected by the leopards (see Chapter 7). This could have been associated with changes in home range size; Norton & Lawson (1985), using VHF telemetry, recorded larger ranges for leopards in the Boland mountains.

Leopards in the Cederberg have some of the largest leopard ranges recorded (Schaller, 1972; Hamilton, 1976; Bertram, 1982; Bailey, 1993; Mizutani, 1998; Marker & Dickman, 2005; Steyn, 2007; Swanepoel, 2008), the largest previously recorded being for male leopards in the Kalahari (1137±578 km^2) (Bothma *et al.*, 1997). The Cape mountains differ vastly from the arid and flat desert sands of the Kalahari, where prey is localised and concentrated primarily around a few river beds and artificial water-holes; this draws animals from afar and may be a determining factor affecting leopard ranges.

Male ranges were significantly larger than females, as found in other studies (Bailey, 1993; Stander & Hayden, 1997; Mizutani & Jewell, 1998). Karoo leopards had larger ranges than in the Fynbos. In the Karoo, I estimated that male home ranges should be *c.* 2.5 times larger than females based on female range size and energy requirements. However, their average observed ranges were 4.4 times larger than those of females. Both grid-cell analyses and selection indices suggest that males were using larger areas than required as a consequence of habitat availability rather than food availability. For example, open areas, constituting almost half the available Karoo habitat, were avoided by leopards. In the Fynbos, however, males utilised an area similar to their expected metabolic range, possibly due to their being less open areas, and more preferred habitats. Thus they did not need to expand their range beyond their energy requirements. Schaller (1972) observed leopards having larger ranges in the open parts of the Serengeti, compared with the woodlands, for the same reason as found here (Bertram, 1982).

4.4.2. Overlap and interaction

Norton & Henley (1987) recorded overlaps of 10 - 57% between male leopards. Their explanation of this being related to 'shifts' in home ranges between individuals corresponds with greater degrees of overlap in my study. On average, male-male ranges overlapped >10% showing a degree of exclusivity (Sandell, 1989). Other studies on leopards have found greater (Norton & Henley, 1987, Stander & Hayden, 1997), or lesser degrees of overlap (Mizutani & Jewell, 1998). However, some overlap is expected for territorial animals such as leopards, where monitoring of neighbouring territorial animals is essential. The GPS radio-collar data from four females, and the camera trapping data, proved inadequate to determine whether their home ranges overlapped. However, GPS tracking and camera-trapping data showed that Karoo and Fynbos leopards did not cross the prominent fault-line between these two areas. The deep valley that runs the length of the divide appears to act as a natural range border for individuals. Topographical features such as rivers also appear to play an important role in defining range boundaries. For example, M1 had the deep fault-line valley as his western border, a prominent river as his eastern border, deep valleys with rivers

as his northern border, and a deep canyon as his southern border. Similar behaviour was witnessed with the other males.

As with other leopard studies (Bailey, 1993; Stander & Hayden, 1997), I found no evidence that leopards were either attracted to or actively avoided making contact with each other. The large ranges suggest that contact was minimized.

4.4.3. Habitat use

Rocky slopes proved the most important habitat for leopards in the Cederberg. Confirmation of this was achieved by using 'distance to rivers' to support these findings. In the Cederberg, most areas <150 m from a perennial or non-perennial river were rocky slopes. Furthermore, in the Karoo, lower elevations, which were selected by leopards, corresponded with deeply incised river gorges. This, together with a preference for mid- to steep slopes, suggests that leopards prefer to move through rocky areas with sufficient cover and good visibility to observe and stalk potential prey. Leopard dietary preferences (see Chapter 7) further confirm their preference for prey inhabiting rough rocky slopes or outcrops. It was unclear whether human habitat or altered landscapes, although only a very small component of the overall habitat, were avoided or not. Individual cases of domestic livestock consumed may have affected these results. Open areas were avoided, possibly due to the threat of being exposed to humans.

4.5. Conclusion

I have shown that leopards in the Cederberg have some of the largest ranges recorded for the species. Leopards in the Karoo had larger ranges than those in the Fynbos, and were avoiding open areas, a dominant habitat in the area. In the Fynbos, open areas were not as common, but were also avoided. This could have been due to human activity in these areas in the Fynbos, for prey appeared to be abundant. However, open areas in the Karoo, which also had a good prey base, were devoid of human activity or habitation. It appeared that leopards in the Cederberg were selecting rocky slopes where their main prey, klipspringers and hyraxes, were easier to stalk and kill. I explore this hypothesis further in Chapter 6 and 7.

Table 4.5. Leopard habitat preferences using resource selection indices and 95% confidence intervals with Bonferroni corrections for 11 leopards in the Cederberg Mountains between 2004 and 2010. Where indices and confidence intervals (CI) >1, habitat selection is indicated in bold at P < 0.05 level, and indices and CIs <1 indicate habitat avoidance. Values overlapping 1 indicate random use.

	Selection index													
			Male vs Female				Summer vs Winter				Karoo vs Fynbos			
	All leopards		Male		Female		Summer		Winter		Karoo		Fynbos	
	CI -	CI +	CI -	CI +	CI -	CI +	CI -	CI +	CI -	CI +	CI -	CI +	CI -	CI +
Habitat type														
Human habitat	-2.047	2.853	-0.945	1.300	-	-	-1.085	1.469	-1.935	3.239	-	-	-0.265	0.725
Open plain	0.285	0.406	0.335	0.418	0.205	0.320	0.238	0.317	0.369	0.482	0.593	0.731	0.493	0.997
Rocky slope	**2.029**	**2.214**	**2.076**	**2.192**	**2.143**	**2.435**	**2.136**	**2.263**	**1.946**	**2.112**	**2.965**	**3.403**	**1.188**	**1.244**
Smooth slope	0.194	0.510	0.247	0.457	0.149	1.878	0.169	0.375	0.294	0.596	0.116	0.407	0.372	0.712
Rocky flat	0.351	0.579	0.322	0.463	0.328	0.510	0.409	0.579	0.336	0.526	0.216	0.445	0.485	0.655
Distance to rivers														
<50 m	**1.583**	**1.957**	**1.792**	**2.095**	**1.192**	**1.543**	**1.713**	**2.044**	**1.473**	**1.812**	**2.539**	**3.186**	**1.161**	**1.353**
50<150 m	**1.058**	**1.257**	**1.071**	**1.231**	**1.067**	**1.272**	**1.114**	**1.291**	**1.014**	**1.194**	0.940	1.267	0.969	1.077
150<1600 m	0.658	0.742	0.620	0.686	0.741	0.835	0.610	0.682	0.723	0.804	0.479	0.579	0.841	0.914
Elevation														
<500 m	0.421	0.894	0.665	1.023	0.144	1.766	0.594	0.993	0.329	0.665	**1.106**	**1.684**	0.309	0.502
501-800 m	0.657	0.865	0.765	0.912	0.565	0.766	0.659	0.818	0.703	0.873	0.998	1.171	0.880	1.088
801 - 1200 m	0.853	1.054	0.812	0.944	0.784	0.927	0.840	0.993	0.915	1.079	0.712	0.870	**1.057**	**1.184**
1201 - 1600 m	**1.871**	**2.858**	**1.839**	**2.493**	**2.252**	**3.209**	**1.988**	**2.763**	**1.961**	**2.743**	-0.794	2.546	**1.162**	**1.334**
1501 - 2000 m	-2.312	4.890	-1.202	3.384	-0.660	2.391	-1.481	4.357	-1.618	3.850	-	-	0.104	1.110
Slope														
<5 degrees	0.318	0.526	0.413	0.566	0.213	0.408	0.325	0.479	0.358	0.533	0.460	0.681	0.417	0.622
5<15 degrees	0.798	0.992	0.826	0.958	0.723	0.896	0.815	0.962	0.823	0.983	0.886	1.107	0.820	0.933
15<25 degrees	**1.242**	**1.792**	**1.298**	**1.672**	**1.349**	**1.983**	**1.351**	**1.773**	**1.241**	**1.687**	**1.194**	**1.893**	**1.152**	**1.391**
25<35 degrees	**1.284**	**2.470**	1.368	2.165	1.636	3.230	**1.432**	**2.337**	**1.381**	**2.355**	0.853	2.429	**1.273**	**1.730**
>35 degrees	0.586	2.861	0.908	2.452	0.622	4.208	0.848	2.578	0.797	2.673	-0.396	3.312	0.850	1.542

Table 4.6. Selection of habitat types in the Cederberg Mountains using Jacobs' index for 11 collared leopards between 2004 and 2010. Positive values (bold) = preference for that habitat (maximal = +1) at $P < 0.05$ level; negative values indicate avoidance (maximal = -1).

	Jacobs index						
		Male vs Female		Summer vs Winter		Karoo vs Fynbos	
	All leopards	Male	Female	Summer	Winter	Karoo	Fynbos
Habitat type							
Human habitat	-0.427	-0.700	0.263	-0.680	-0.212	-1.000	-0.631
Open plain	-0.582	-0.549	-0.684	-0.657	-0.499	-0.322	-0.155
Rocky slope	**0.694**	**0.702**	**0.713**	**0.732**	**0.648**	**0.726**	0.358
Smooth slope	-0.512	-0.512	0.007	-0.604	-0.416	-0.623	-0.315
Rocky flat	-0.416	-0.489	-0.490	-0.388	-0.450	-0.561	-0.312
Rivers							
<50 m	0.350	0.407	0.193	0.386	0.304	0.164	0.145
50<150 m	0.104	0.100	0.111	0.132	0.070	-0.391	0.017
150<1600 m	-0.327	-0.376	-0.216	-0.383	-0.260	-0.799	-0.117
Elevation							
<500 m	-0.081	-0.097	-0.024	-0.132	-0.371	0.196	-0.432
501-800 m	-0.239	-0.128	-0.270	-0.213	-0.170	0.073	-0.361
801 - 1200 m	-0.030	-0.102	-0.145	-0.070	-0.003	-0.185	-0.008
1201 - 1600 m	0.448	0.431	**0.550**	0.480	0.475	-0.068	**0.608**
1601 - 2000 m	0.043	0.044	-0.074	0.182	0.056	0.000	0.266
Slope							
<5 degrees	-0.486	-0.418	-0.601	-0.506	-0.462	-0.360	-0.360
5<15 degrees	-0.091	-0.094	-0.179	-0.097	-0.084	-0.004	-0.106
15<25 degrees	0.262	0.248	0.317	0.280	0.239	0.262	0.159
25<35 degrees	0.345	0.312	0.468	0.347	0.342	0.265	0.235
>35 degrees	0.282	0.269	0.435	0.279	0.285	0.192	0.097

CHAPTER 5

Leopard abundance and densities as determined by camera trapping and GPS telemetry

Summary

Persecution and habitat loss have resulted in the widespread eradication of many large predators. Whilst leopards are the last remaining large predator in the Western Cape, their abundance and densities remain unknown. I outline the systematic use of camera trapping techniques, coupled with modern GPS radio-collars, to assess their use in quantifying leopard densities in the Karoo biome, Cederberg Mountains. Density estimates in the Fynbos were made using home range data from GPS radio-collars. A total of 193 leopard photographic captures in 12,127 trap nights showed that male trapping success (0.97/100 trap nights) was higher than female trap success (0.38/100 trap nights). Seven adults (2 males, 5 females) and 3 sub-adults were recorded during four camera trapping surveys, one each in summer and winter over 2 years. Abundance estimates generated by the program CAPTURE were 5.8 – 11.6. Using four different buffer calculation methods, densities in the Karoo varied between 0.25 – 0.99 leopards/100 km^2. Fynbos densities were between 1.8 – 2.3 leopards/100 km^2. GPS home range data improved density estimates; densities just based on camera trapping data should be viewed with caution. However, camera traps provide valuable ancillary data of relative prey abundance and movement of leopards not tracked by GPS radio-collars.

5.1. Introduction

As recently as 300 years ago, leopards in the Western Cape occurred sympatrically with a greater faunal assemblage, including lions, brown hyaenas, spotted hyaenas *Crocuta crocuta*, buffalo *Syncerus caffer*, black rhinoceros and elephants (Shortridge, 1934; Skead, 1980). Other than leopards, all of these were extirpated by loss of habitat and persecution by European settlers.

The conservation of threatened populations occurring at low densities, such as tigers, jaguars, snow leopards and leopards, relies on accurate population

estimates (Karanth, 1995; Silver *et al.*, 2004; Wang & Macdonald, 2009). Solitary, large carnivores inhabiting remote areas are notoriously difficult to study. Confirmation of densities using a combination of methods could alleviate some of the problems associated with estimating population densities. Techniques such as spoor or track counts (Stander, 1998; Silveira *et al.*, 2003; Gusset & Burgener, 2005), microsatellite DNA analysis using scats (Kohn *et al.*, 1999; Bellemain *et al.*, 2005; Creel *et al.*, 2009) and calculating densities using home ranges of radio-tagged animals (Hamilton, 1976; Bailey, 1993; Bothma *et al.*, 1997; Stander & Haden, 1997; Marker & Dickman, 2005) have been used as indicators of density with varying success.

Tracking of leopards by their spoor in extreme rocky habitat is difficult if not impossible. Furthermore, use of spoor to estimate carnivore populations is unreliable (Karanth & Nichols, 1998). Track counts were therefore ignored, while scats, fresh or old, were not easy to find, thereby excluding a robust survey using DNA analyses. Camera-trapping capture-mark-recapture (CMR) studies have been used to study elusive carnivores elsewhere (Karanth, 1995; Karanth & Nichols, 1998). Because leopards, like tigers and jaguars, have unique body patterns, individuals can be readily identified from photographs, providing essential data on population numbers and their corresponding densities (Karanth & Nichols, 1998; Henschel & Ray, 2003). These studies also provide information on other species that utilize the same habitat.

To date, little research has been conducted on the mountain leopards of the Cape. Three studies over the past 25 years have resulted in varying and inconclusive density estimates (Norton *et al.*, 1986, Norton & Henley, 1987; Stuart & Stuart, 1991). Two of these studies took place in the Cederberg Mountains, with one producing density estimates of 6 - 9 leopards/100 km^2 based on the home ranges of three male leopards determined from VHF radio tracking (Norton & Henley, 1987). The second study estimated 2 leopards/100 km^2, making use of spoor counts after their camera-trapping study failed (Stuart & Stuart, 1991). Considering the limitations of VHF tracking (McCarthy *et al.*, 2005) and using spoor, these data must be viewed with caution.

Although camera trapping studies provide an effective, non-invasive way of obtaining abundance estimates of many species of felids, they have recently been

shown to yield overestimates of carnivore densities (Soisalo & Cavalcanti, 2006; Dillon & Kelly, 2008). This is often due to lack of reliable information on home range sizes, leading to incorrect camera spacing (Dillon & Kelly, 2007). Furthermore, density estimates can be miscalculated due to incorrect buffers used to determine the effective survey area, resulting in population overestimates of up to, and possibly more than, 74% (Soisalo & Cavalcanti, 2006).

In order to address pitfalls of various methods used on their own, I combined a camera trapping study with home range analyses using GPS radio collars, to obtain density estimates for leopards in the Cederberg Mountains. My aims were: (i) to estimate abundance and density of leopards in the Cederberg using remote camera trapping techniques; (ii) to assess suitable techniques for estimating buffer areas for camera trapping surveys; (iii) to compare leopard densities using GPS radio collar and camera trapping data; and (iv) to estimate leopard densities using collar data only.

5.2. Methods

5.2.1. Use of remote infra-red camera traps in studying leopards

See Chapter 3.

5.2.2. Leopard capture and immobilisation for monitoring using GPS radio-collars

See Chapter 3.

5.2.3. Leopard home range determination

See Chapter 4.

5.2.4. Calculating leopard densities using home range size

Resulting density estimates for leopards using home range were calculated using their 95% MCP ranges. The total number of adult male ranges able to fit within the available area took into account overlap calculated using temporal and spatial parameters. Degree of overlap was only considered when contiguous and overlapping animals were monitored at the same time. Although Bailey (1993) found up to 6 females within an adult male's home range, 2 – 3 were considered

the norm (Hamilton, 1976; Mizutani & Jewell, 1998). I therefore considered the total number of adult females within the same area as 2.5 per male. Females showed no signs of overlap based on camera trapping results and results from other studies (Schaller, 1972; Bertram, 1982; Mizutani & Jewell, 1998).

5.2.5. Survey area buffer calculations

Leopard density estimates were obtained using four different methods of calculating the buffers around the survey area. As outlined in Chapter 3, the effective survey area was calculated using circular buffers added to camera station points (Silver *et al.*, 2004; Soisalo & Cavalcanti, 2006; Dillon & Kelly, 2008). Buffers were calculated using (i) the mean maximum distance moved (MMDM), (ii) the full mean maximum distance moved (FMMDM), (iii) the average of actual MMDM as determined by GPS-collared animals divided by two (providing the home range radius) and (iv) the radius of mean actual home ranges as determined by GPS radio tracking of individuals within the survey area using $A = \pi r^2$, where A = home range area using 95% MCP, and r = the buffer width.

5.3. Results

5.3.1. Camera trapping

Four camera trapping surveys with a total of 7987 trap nights resulted in 96 photographic captures of 13 different leopards i.e. seven adults (2 male, 5 female), three sub-adults and 3 cubs under the age of 3 months (Table 5.1). Average camera trapping success across the four surveys was 1.2±0.2 leopards per 100 trap nights. These data were combined with *ad hoc* surveys from May 2004 – December 2007 to give a total of 193 leopard photographic captures in 12,127 trap nights, with an overall trap success of 1.6 leopards per 100 trap nights. Male trap success was 0.97/100 trap nights (n = 118), female success 0.38/100 trap nights (n = 46); this excludes 29 captures for which the sex was unidentifiable.

Of the three leopards identified in this study as sub-adults, two of their ages were confirmed when captured during the study and identified as one male (*c.* 1.5 year) and one female (*c.* 1 year). Four of the seven adults were confirmed as mature individuals when live-captured and collared. Two of the sub-adult leopards were not recorded again after February 2007, suggesting that they had dispersed

beyond the study area or died. The only sub-adult I was able to continue monitoring was the male M6. He was regularly photographed in the same area from the age of *c.* 1 year in May 2005 until October 2007. During this time, no adult males were photographed in that area. However, in March 2008 a new adult male, M13, replaced M6. M6 was later recorded by several camera-trap stations some 20 km north-west of his former range, suggesting he had established a new territory. This was the only time I recorded a sub-adult leopard surviving to adulthood in the Cederberg in six years.

Juvenile leopards were rarely caught on film. One 3-month-old cub was photographed in January 2005 and two 3-month-old cubs were photographed with their mother in January 2007. Identikits were not possible for these juveniles, and so I was not able to monitor their survival or dispersal patterns.

Calculation of buffers

Using a one-way ANOVA, buffer widths for the camera trapping survey differed significantly according to the different methods ($P < 0.05$; $df = 3$; $F = 7$; $r^2 = 0.64$) (Table 5.2). The MMDM distance moved by leopards captured at least twice by cameras was 6.0 km (survey 1), 11.5 km (survey 2), 7.5 km (survey 3) and 5.1 km (survey 4), with an overall mean of 7.5±1.4 km. The FMMDM was calculated as MMDM x 2, where the mean for the four surveys was 15.1±2.8 km. Combined home ranges (95% MCP) of all Karoo leopards, where camera surveys were

Table 5.1. Captures of male (M), female (F) and sub-adult (SA) leopards in the four camera trapping surveys, with *N* the total leopards captured, *P-hat* the capture probability, and the population size (±SE) as determined by the program CAPTURE's M(h) model. Surveys 1 (November 2004 – March 2005) and 4 (November 2006 – March 2007) were in the summer, surveys 2 (May 2005 – September 2005) and 3 (May 2006 – September 2006) in the winter.

Survey	Trap days	Captures*	*N***	M	F	Sub-adults	Population size ± SE	*P-hat*	Captures/ 100 trap days	Closure test	
										z-value	*P*-value
1	2353	13	6	2	3	1	8.1±3.3	0.15	0.89	1.13	0.87
2	2120	17	9	2	4	3	11.6±3.4	0.13	1.65	0.47	0.68
3	1946	14	6	2	2	2	6.1±2.4	0.19	0.92	0.41	0.66
4	1568	12	4	2	1	1	5.8±4.2	0.17	1.40	0.65	0.74

* In surveys 1 and 2, one 'occasion' = 4 days; in surveys 3 and 4, one 'occasion' = 10 days.
** Juveniles were excluded from analyses.

Table 5.2. Camera trapping surveys 1 – 4 with the respective survey areas, buffers, methods of buffer calculation, effective survey areas and resulting leopard densities based on CAPTURE abundance figures and four methods of buffer calculation, viz. Maximum Mean Distanced Moved (MMDM) from camera data, Full Maximum Mean Distanced Moved from cameras, MMDM as determined by GPS collar data and the actual buffer radius as determined by GPS collar home ranges (AHR).

Survey	Area (km^2)	Buffer calculation*	Buffer width (km)	Effective survey area (km^2)	CAPTURE abundance	Density/100km^2
1	374	MMDM	6.0	872	8.1±3.3	0.93±0.38
		FMMDM	12.1	1773	8.1±3.3	0.46±0.19
		GPS collar MMDM	11.4	1660	8.1±3.3	0.49±0.20
		GPS collar AHR	16.9	2627	8.1±3.3	0.31±0.13
2	374	MMDM	11.5	1676	11.6±3.4	0.69±0.20
		FMMDM	23.0	3915	11.6±3.4	0.30±0.09
		GPS collar MMDM	11.4	1660	11.6±3.4	0.70±0.20
		GPS collar AHR	16.9	2627	11.6±3.4	0.44±0.13
3	247	MMDM	7.5	885	6.1±2.4	0.69±0.27
		FMMDM	15.0	1963	6.1±2.4	0.31±0.12
		GPS collar MMDM	11.4	1406	6.1±2.4	0.43±0.17
		GPS collar AHR	16.9	2288	6.1±2.4	0.27±0.10
4	247	MMDM	5.1	583	5.8±4.2	0.99±0.72
		FMMDM	10.3	1251	5.8±4.2	0.46±0.34
		GPS collar MMDM	11.4	1406	5.8±4.2	0.41±0.30
		GPS collar AHR	16.9	2288	5.8±4.2	0.25±0.18

conducted, resulted in an outer polygon with a total area of 1146 km^2. Here the average MMDM for the 4 leopards was 22.8 km. The distance used for the circular buffer was calculated by dividing this MMDM by 2, giving a buffer radius of 11.4 km to be added to camera stations in surveys 1 - 4. When calculating the radius using the 95% MCP home range size, the buffer (radius) was 16.9 km.

Leopard population size

In calculating leopard abundance, the program CAPTURE selected the Constant Capture Probability Model, M(o), as the best fitting for all four surveys (1.0). However, this model assumes no sources of variation in capture probabilities and has been criticised for being over-simplistic for wild populations (Jackson *et al.*,

2005). I used M(h) (0.87±0.02), the heterogeneity model selected by CAPTURE which takes into account variation in capture probabilities in animals because of differences in sex, age, dominance and activity.

Capture probabilities of 0.16 ±0.01 for all leopards were low, but consistent. Throughout the four surveys population size for the four surveys varied between 4 and 9 leopards, of which 3 to 6 were adults. Population closure was recognised for each of the sampling periods, with z = -0.67±0.16 and P = 0.74±0.05.

Faunal diversity and capture frequency

Camera trapping produced 4403 photographs of mammals; this excluded duplicate photographs from opposite cameras. Livestock accounted for 707 of these photographs. I had 7761 false triggers which included people, dogs, birds, bats, small rodents, unidentified animals or blank photographs caused by heat or movement such as bushes, dust or rain. Relative abundance of mammals captured during camera-trapping surveys were calculated using 'capture events', where more than one photograph of a given species at a unique station on a single day was regarded as 1 capture event (Table 5.3). Total captures for non-domesticated animals was 2532.

5.3.2. Densities using home ranges determined by GPS telemetry

As I showed in Chapter 4, home ranges calculated using 95% MCPs varied from 74 to 910 km^2 (242±74 km^2). Since Fixed Kernel ranges were 1.27±0.06 times larger, I used 95% MCP home ranges to calculate leopard densities, not FKs for density estimates. Both male and female leopards in the Karoo had larger home ranges than Fynbos leopards, and as no overlap was recorded between Karoo and Fynbos leopards, densities using home ranges were calculated separately for each biome. Males (n = 2) and females (n = 2) monitored in the Karoo had ranges of 428 and 910 km^2 (669±24 km^2) and 100 and 203 km^2 (152±52 km^2) respectively. Although an overlap of 23.9% occurred between males, it was not temporally comparable. However, only 2 adult males were recorded for the duration of the study. Using a ratio of 2.5 females per male, the population of adult leopards in the Karoo was seven. It is likely that M1's expansion of his range (Chapter 4) was into a third Karoo male's range, suggesting a possible population

Table 5.3. Mammal captures during Cederberg camera trapping surveys 2004-2007. Capture events indicates the number of captures at all camera stations, excluding duplicate captures on the same day.

Species	Common name	Capture events
Oreotragus oreotragus	Klipspringer	385
Papio ursinus	Chacma baboon	311
Procavia capensis	Rock hyrax	307
Oryx gazelle	Oryx	216
Aonyx capensis	Small grey mongoose	208*
Atilax paludinosus	Water mongoose	
Panthera pardus	Leopard	193
Hystrix africaeaustralis	Cape porcupine	132
Lepus capensis	Cape hare	132*
Lepus saxatilis	Scrub hare	
Raphicerus melanotis	Cape grysbok	113
Genetta genetta	Small spotted genet	95*
Genetta tigrina	Large spotted genet	
Proteles cristatus	Aardwolf	77
Felis silvestris	African wild cat	76
Orycteropus afer	Aardvark	66
Equus zebra	Cape mountain zebra	53
Pelea capreolus	Grey rhebok	40
Caracal caracal	Caracal	28
Pronolagus rupestris	Smith's red rock rabbit	28
Antidorcas marsupialis	Springbok	27
Mellivora capensis	Honey badger	25
Canis mesomelas	Black-backed jackal	9
Raphicerus campestris	Steenbok	5
Ictonyx striatus	Striped polecat	4
Vulpes chama	Cape fox	2

* Combined figures for hares, mongooses and genets

of 10 - 11 (10.5) adults. Since the Karoo study area was 1728 km^2 and the average home ranges of two collared males was *c.* 670 km^2, three males seemed a good estimate for this area. Determination of female densities based on their average home range of *c.* 150 km^2 and no overlap resulted in a possible 11 - 12 females inhabiting this area.

Male leopards in the Fynbos had a mean home range of 170±30 km^2 (n = 5), females 82±8 km^2 (n = 2). The maximum male-male overlap recorded for the same period was 18% for M8 and M9, while the average overlap was 10%. I had no data on whether female home ranges overlapped. The Fynbos study area was

1359 km^2, allowing for at least 8 males with no overlap and 9 males with a 10% overlap. Based on 2.5 females/male, the total adult Fynbos population would be 28 – 32. Using the average home range for collared females and no overlap, this would be 25 – 27 adult leopards.

5.4. Discussion

5.4.1. Density estimates for large carnivores

Reliable population density estimates for large carnivores are essential for their conservation (Smallwood & Fitzhugh, 1995; Gusset & Burgener, 2005). The difficulty in studying elusive animals in rugged environments has made the use of remote-triggered infra-red cameras to monitor individually-identifiable mammals, such as leopards, a useful and effective way to obtain estimates on population abundance and activity. Modern infra-red remote camera systems are a large improvement on previous systems, such as those using mechanical tread plates with film cameras. In the Cederberg, for example, only one leopard photograph was captured during a year-long study using 5 such camera systems (Stuart & Stuart, 1991). Radio telemetry data have also been used to provide density estimates for leopards; however, the use of VHF telemetry in mountainous areas can underestimate home range size of far-roaming animals (McCarthy *et al.*, 2005). This may explain why Norton & Henley's (1987) home range estimates for male leopards of between 42.1 and 66.8 km^2 in the Cederberg Mountains, and subsequent density estimate of 6 - 9 adult leopards/100 km^2, appears to be an underestimation of home range size and overestimation of density. I will discuss this further in Chapter 8, as it is possible that conditions have changed sufficiently to warrant these differences.

5.4.2. Use of camera traps to estimate prey abundance

The limitations of camera traps lie in their placement, their limited capture range (*c.* 10 m), and the statistical framework used to analyse the data (Stein *et al.*, 2008; D. Borchers, pers. comm., 13/09/2010). Absolute measures of abundance are also only possible for individually identifiable animals (Karanth & Nichols, 1998; Silver *et al.*, 2004). However, having a camera trap act as a dedicated 24 hr observer placed in the field, day or night, rain or shine, is a useful monitoring tool.

My results for other mammal species suggest klipspringers, baboons and hyraxes were the most abundant prey species. Apart from baboons, which are a formidable prey item and seldom preyed on by leopards in the Cape (Norton *et al.*, 1986; Ott *et al.*, 2007; Martins *et al.*, 2010), these data support the dominance of the two prey species in my leopard diet study (see Chapter 7). The fact that leopard photographic captures accounted for *c.* 8% of all captures is probably a function of well-selected trap placement rather than abundance. Further work is required to utilize camera trapping data in a more meaningful way for species without clear identifiable markings.

5.4.3. Capture probabilities and leopard abundance from camera trapping surveys

The probability of leopard capture was low, but comparable to camera trapping studies of large felids conducted elsewhere (Karanth & Nichols, 1998; Silver *et al.*, 2004; Balme *et al.*, 2009). Between 4 and 9 leopards (mean 6.3±1.0) were identified in the four surveys. The resulting abundance estimates by the program CAPTURE produced similar estimates to the average number of animals captured (7.7±3.4). However, female leopards were not photographed as frequently as males (69% male; 31% female), suggesting under sampling of females due to low trapping success. This trend was also observed for live-captures; 7 females (32%) were captured in cage-traps, compared to 15 males (68%). Camera trapping data in the Gouritz mountain region of South Africa have yielded similar male-female biases (Q. Martins, unpublished data). Several studies have shown male-biases, when the opposite should be true (Wallace *et al.*, 2003; Silver *et al.*, 2004; Soisalo & Cavalcanti, 2006). It has been suggested that females are more shy and avoid human-made paths (Salom-Pérez *et al.*, 2007). However, this could not account for the sex bias in my study, since human-made paths were scarce or non-existent in the Karoo.

The paucity of female photographic captures was clearly not a reflection of their abundance or a tendency to avoid traps, since I recorded more females than males in the population and did not observe tracks of any females showing signs of avoidance by walking round a camera or cage-trap. The bias towards male photographs may simply be because, unlike males, females move in a more

undefined manner (Kure, 2003), and do not follow paths or tracks where cages and cameras were often placed as regularly.

5.4.4. Leopard densities

Provided animals are individually identifiable, camera trapping has proved to be an effective monitoring technique capable of producing accurate population estimates; however, actual density estimates are more difficult to determine due to inaccurate estimates of the effective survey area. Several studies have raised concerns of either over- or underestimation of population densities based on inaccurate effective sample areas (Siosalo & Cavalcanti, 2006; Dillon & Kelly, 2008; Balme *et al.*, 2009). My comparisons of four methods of determining the effective survey area confirmed the variability in buffer size calculations and the resulting variation in densities. For instance, for the four different methods, densities for a particular survey varied from 0.25 – 0.99 leopards/100 km^2, suggesting the leopard population in the Karoo, where the camera study was conducted, could be between 4 and 17 leopards. Choosing the most suitable method was speculative. Intuitively, densities determined by GPS collar home range results were the most accurate. Similar conflicting views were experienced despite use of multiple methods (Soisalo & Cavalcanti, 2006; Balme *et al.*, 2009). Furthermore, under-sampling of females confounded the issue further.

Using home range estimates for males and females from the GPS collars, I estimated the adult leopard population in the Karoo to be 10 – 15, i.e. a density of 0.6 – 0.9 leopards/100 km^2. This suggests that buffers calculated using MMDM from cameras gave the best fitting densities for the Karoo, a method also considered accurate by Silver *et al.* (2004) and Balme *et al.* (2009). However, considering the variability, these results should be viewed with caution.

Leopard densities in the Fynbos using home range data were higher (1.8 – 2.3 leopards/100 km^2). Due to the significant differences between the two biomes, I used their respective densities to estimate the population in my study area, which resulted in a total of 35 – 47 adult leopards, with overall density being 1.1 – 1.5 leopards/100 km^2.

Table 5.4. Adult leopard density estimates in different habitats of sub-Saharan Africa, using track counts, camera trapping, VHF and GPS telemetry.

Study*	Density/ 100 km²	Location	Method	Habitat
1	0.5	Kalahari Gemsbok National Park, S.A.	VHF	Arid savanna
2	0.6 - 0.9	Cederberg, S.A.	GPS/Camtrap	Arid mountain
3	0.8	Boland, S.A.	VHF	Mesic mountain
4	1.5	Kaudom Game Reserve, Namibia	VHF	Arid savanna
5	1.8 - 2.3	Cederberg, S.A.	GPS	Mesic mountain
6	1.9	Waterberg, S.A.	VHF	Mountain savanna
7	6.0 - 9.0	Cederberg, S.A.	VHF	Mesic mountain
8	6.9 - 7.5	Northern Tuli Game Reserve, Botswana	GPS/Camtrap	Savanna
9	*c.* 7.0	Phinda, Kwazulu Natal, S.A.	VHF/Camtrap	Savanna
10	9.5 - 16.4	Kruger National Park, S.A.	VHF	Savanna
11	20.0 - 22.2	Matopos National Park, Zimbabwe	Tracks	Hill/savanna
12	23.8	Londolozi Game Reserve, S.A.	Observation	Savanna

*1: Bothma & Le Riche, 1997; 2: Q. Martins, present study; 3. Norton & Lawson, 1985; 4: Stander & Haden, 1997; 5: Q. Martins, present study; 6: Grimbreek, 1992; 7: Norton & Henley, 1987; 8: Steyn, 2008; 9: Balme *et al.*, 2009; 10: Bailey, 1993; 11: Smith, 1977; 12: Le Roux & Skinner, 1989.

Leopard densities in the Karoo were one of the lowest recorded. Overall, densities were comparable to the low density populations in Namibia (Stander & Haden, 1997; Marker & Dickman, 2005) and the Kalahari (Bothma *et al.*, 1997) and Waterberg Mountains (Grimbreek, 1992) (Table 5.4). The lack of larger predators could have an influence on their behaviour, resulting in larger ranges (Creel *et al.*, 2001).

5.5. Conclusion

I have demonstrated that using GPS radio-collar data in combination with camera trapping surveys provides better population density estimates than by camera trapping alone. The advantage of combining the two approaches is that it overcomes problems of under-recording animals not captured on camera traps. Furthermore, although not absolute, camera data provide a useful means of understanding the prey base, and are able to produce a rough index of relative abundance of prey, particularly in habitats frequented by target species such as leopards. My results have demonstrated that leopards in the Cederberg occur at very low densities, particularly in the Karoo. These data suggest that unless a significant proportion of the population are monitored using telemetry, population estimates are to be viewed with caution, especially when dealing with threatened

species. Furthermore, extrapolating the densities recorded here suggest that the population of leopards inhabiting the mountains of the Western Cape, based on their distribution and available habitat, may be as low as a few hundred adult animals.

CHAPTER 6

Movement, activity and hunting behaviour of mountain leopards

Summary

Few data are available on the activity of leopards in mountain habitats where the co-existence of competing large predators is absent. Large carnivores are believed to influence the activity and movement of smaller competitors. Human activity has also been known to alter carnivore behaviour. Understanding the activity and movement patterns of leopards provides insight into understanding complex behaviour patterns which are useful in the conservation of the species. I used remote camera traps and GPS radio-collars to determine whether leopards in the Cederberg were diurnal or nocturnal, whether there were seasonal or sexual differences in their behaviour. Furthermore, I related activity to hunting behaviour and whether leopards avoided human habitats, roads or paths. 77% of camera trap photographs were at night, with a strong male bias (69%) in captures. Daily displacement using 1 location per day showed males moving significantly further than females (4091 m vs 2963 m; P<0.0001). However, multiple locations (≥6) showed no difference in daily distance moved suggesting males move in a more linear fashion to females. Human habitation appeared not to influence leopard movement. Leopards were hunting diurnal prey species at night, mostly at the darkest times of the lunar cycle. I found leopards to be predominantly nocturnal in the Cederberg seemingly unaffected by humans or lack of competing predators.

6.1. Introduction

Monitoring activity and movement patterns for elusive species is difficult. As a result we know little about the activity of leopards (Nowell & Jackson, 1996; Sunquist & Sunquist, 2002). Because activity is an important component of behavioural ecology, limited or no data impedes a thorough understanding of the species. However, remote sensing and monitoring of populations has been facilitated by technological improvements, including the advent of infra-red camera traps and GPS radio-collars, which can be used to explore the movements and activity of elusive large carnivores. Some early studies, for instance, could only

collect diurnal activity due to the practical problems associated with VHF tracking at night (Bailey, 1993; Cavalcanti & Gese, 2009).

Large carnivore guilds often result in spatial or temporal separation in animal activity and movements. There may even be significant variation in food preferences so as to avoid competition. Where large predators co-exist, leopards have been shown to avoid tigers by being more active during the day, and feeding on different size prey (Seidensticker, 1976; Azlan & Sharma, 2006). In African savannas, leopards avoid deleterious interactions by hoisting their prey into trees out of reach of competing predators (Kure, 2003). They also select different habitats to those favoured by larger competitors, such as lions (Schaller, 1972). In the Cape, leopards have become the apex predator, and the absence of large competitors facilitates studies on human influence (e.g. human-wildlife conflict), inter- and intrasexual species interaction, and foraging based on leopard movement patterns and activity.

In this chapter, my aims were to: (i) determine daily, seasonal and sexual variation in leopard activity patterns using camera trap capture and GPS radio-collar data; (ii) determine the efficacy of activity count data from GPS collars; (iii) evaluate whether activity was correlated with human habitation; and (iv) use activity data to unravel aspects of leopard hunting behaviour.

6.2. Methods

6.2.1. Study area

See Chapter 2.

6.2.2. Activity using camera trapping

See Chapter 3.

I used all leopard photographs captured in the Karoo until March 2010 to calculate seasonal and sexual differences in activity. When comparing male vs female activity patterns, only adult leopards were considered for analyses. I identified differences in activity for leopards as well as key prey species from the date and time stamped on each photograph; data were excluded where dates/and or time were not clear on photographs taken with film cameras.

6.2.3. Leopard capture and immobilisation

See Chapter 3.

6.2.4. Monitoring activity using GPS collar data

Distance moved and activity patterns

Collars had varying schedules (Chapter 3) combined with different fix rate success (Chapter 4). For day/night distance moved, I used distance between GPS locations from all leopards for points separated by ≥ 4 hrs and ≤ 8 hrs. The cumulative distance for a particular day/night period was divided by the number of hours over which points were taken and multiplied by 12. I excluded all points overlapping sunrise/sunset i.e. 06.30 and 18.30.

Seasonal variation for leopards in different biomes was calculated using one GPS location per day. One location per day was also used to observe maximum distance moved or maximum displacement over 24 hrs. The means±SE for each individual, season, sex and biome were calculated and non-parametric Mann-Whitney analyses conducted to test for significant differences between groups.

Two leopards, M11 and F10, were tracked on an hourly basis in the Fynbos for 13 and 19 non-consecutive days between 21/07/2008 and 24/05/2009. I used these data to assess the accuracy of using only 1 location per day. For each of M11's and F10's intensive tracking periods, I determined distance moved using 1 location per day; 6 evenly spaced locations per day; and 24 locations per day. Where an hourly GPS schedule was set and 24 locations were not captured, I used data with a minimum of 18 points for that day. These data were converted to distance moved/day by dividing the total distance for that day by the number of points and multiplying it by 24.

Use of paths and the influence of human activity

Using ArcGIS, I created a buffer of 25 m around hiking paths, 50 m for roads and 50 and 100 m for areas with human habitation and/or activity throughout my study area. All leopard GPS locations were overlayed onto this map, and points counted that intersected with the buffered areas. These were then sorted for day/night.

Activity sensors

The Vectronic's GPS collars I used had dual-axis motion sensors using an accelerometer, which separately measured the true acceleration of the collar in 2 orthogonal directions 6 - 8 times per second. The acceleration values recorded during the time interval between 2 successive activity fixes were averaged, providing values on the X-axis and Y-axis ranging from 0 to 255 over a 5 minute period. Because these values may vary considerably due to factors such as differences in collar tightness between individuals, but not for an individual, results were compared using percentages when making intraspecific comparisons (Moen *et al.*, 1996; Gervasi *et al.*, 2006). Data were analysed using the computer software programme provided by collar manufacturer Vectronic Aerospace GmbH (Berlin, Germany) (Activity Pattern, version 1.0). Because the remote downloading of activity data consumed considerable battery power from the collar, I only obtained activity data once the collar was retrieved.

6.2.5. Hunting and influence of moonlight

Kills found using GPS cluster analysis as well as clusters identified as kills based on time of the fixes exceeding 24 hrs, allowed for estimation of time of kill (Chapter 7). I identified all kills made at night in order to assess the influence of moonlight on hunting success of leopards, as well as what species of prey were being killed. Prey were identified as being diurnal or nocturnal. Kill dates were compared with the phases of the moon for those nights. I classified these lunar phases based on the relative amount of light emitted, starting with the least amount of light: (i) new moon; (ii) half-new; (iii) half; (iv) half-full; and (v) full. Kills were considered as new moon, half (first & third quarter) and full moon when taking place within two days either side of these respectively. Half-new and half-full fell between these.

6.3. Results

6.3.1. Camera trap activity results

Between 2004 and 2010, I captured 379 leopard photographs; date and time were clearly identifiable for 339, and these were used to determine differences in daily activity, seasonal variation and temporal variation between males and females (Fig. 6.1). I took average sunrise to be 06.30, average sunset 18.30. Of the 339

photographs, 23% (77) were in the day, 77% (262) in the night. There were similar numbers of captures in summer and winter (184 vs 155), as was the pattern of nocturnal activity in summer and winter (83% vs 71%). Diel trends for summer and winter appear similar other than the decrease in activity after 18.00 in winter (Fig. 6.1b). Of these photos, 282 were of adults; 69% (194) were adult males, 31% (88) adult females (Fig. 6.1c).

Prey species captured on camera were recorded in Chapter 5 (Table 5.3). The key prey species for leopard in the Cederberg were klipspringers and rock hyraxes (see Chapter 7). These were predominantly diurnal; 89% (n = 412) and 98% (n = 545) respectively of the captures were during the day. Grysbok and porcupine *Hystrix africaeaustralis* were nocturnal; 89% (n = 101) and 98% (n = 231) of the captures were at night. Grey duiker were not photographed, but were observed feeding during the day and night.

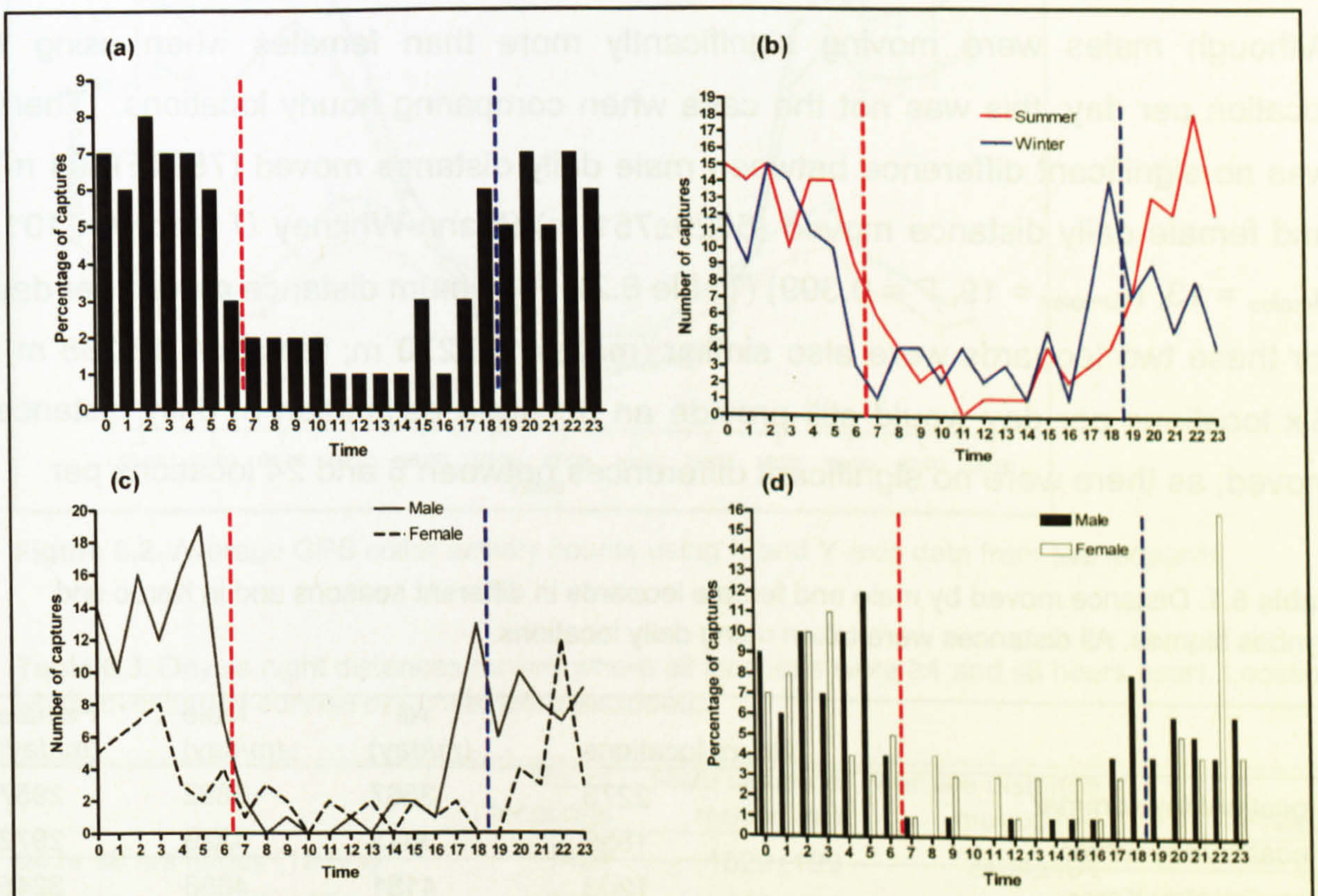


Figure 6.1. Camera activity graphs for leopards showing (a) total percentage of captures; (b) number of captures in summer and winter; (c) number of male vs female captures; and (d) percentage male vs female captures. Red dashed line indicates average sunrise; blue dashed line, sunset.

6.3.2. Distance moved

Sexual variation in leopard movement was noted both in daily distance moved as well as differences in diel movement parameters.

Consecutive GPS locations – 1 location per day

For consecutive daily locations, males moved significantly further per day than females (4091±69 m vs 2963±57 m) (Mann-Whitney *U* test: $U = 1{,}634{,}000$, $n_{males} = 2716$ $n_{females} = 1416$, $P < 0.0001$). Similarly, the maximum distance moved by males was 30,631 m vs 11,574 m for females, where the mean±SE maximum displacement for individuals was 16,203±2550 m for males and 10,960±490 m for females. I found no significant differences between or within biomes or seasons (Table 6.1).

Multiple locations versus 1-daily GPS locations

Although males were moving significantly more than females when using 1 location per day, this was not the case when comparing hourly locations. There was no significant difference between male daily distance moved (7891±1304 m) and female daily distance moved (6629±751 m) (Mann-Whitney *U* test: $U = 101$, $n_{males} = 13$, $n_{females} = 19$, $P = 0.399$) (Table 6.2). Maximum distance moved per day for these two leopards were also similar (male = 15,270 m; female = 12,288 m). Six locations per day would still provide an accurate estimation of daily distance moved, as there were no significant differences between 6 and 24 locations per

Table 6.1. Distance moved by male and female leopards in different seasons and in Karoo and Fynbos biomes. All distances were taken using daily locations.

	No. of locations	All (m/day)	Male (m/day)	Female (m/day)
1 location/day summer	2273	3567	3892	2957
1 location/day winter	1859	3873	4329	2972
1 location/day Karoo	1203	4181	4686	3245
1 location/day Fynbos	2929	3509	3851	2844
1 location/day Karoo summer	526	3621	4025	3152
1 location/day Karoo winter	677	4615	5062	3371
1 location/day Fynbos summer	1747	3550	3861	2870
1 location/day Fynbos winter	1182	3448	3834	2812

day for males (Mann-Whitney *U* test: $U = 172$, n = 13, P = 0.31) and females (Mann-Whitney *U* test: $U = 134$, n = 19, P = 0.179).

Table 6.2. Distances moved by two leopards in the Fynbos using multiple locations. Data were included for all days with more than 18 hourly locations per day.

ID	No. days	1 location/day (m)	6 locations/day (m)	24 locations/day (m)
M11	13	4137	6658	7891
F10	19	2361	5063	6629

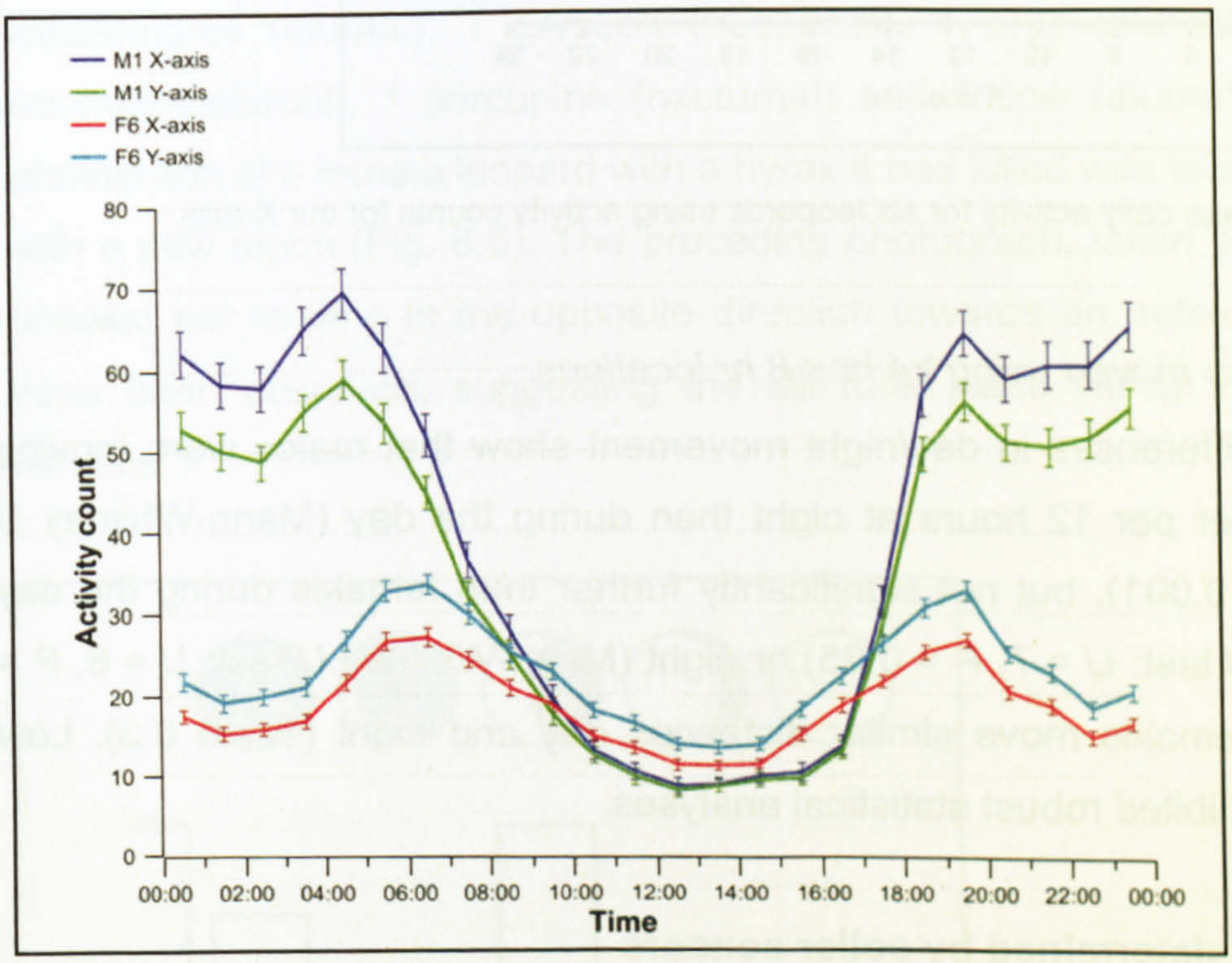


Figure 6.2. Average GPS collar activity counts using X and Y-axis data from two leopards.

Table 6.3. Day vs night distances moved where all locations were ≥4 and ≤8 hours apart. Locations which overlapped sunrise or sunset were excluded.

	No. of locations	Male distance moved (m)	Female distance moved (m)	P-value*
≥4 hr ≤8 hrs m/day (12 hrs)	1481	1820±199	2104±191	0.35
≥4 hr ≤8 hrs m/night (12 hrs)	2754	4128±475	2506±604	0.16
P-value*		0.001	0.69	

* P-value for Mann-Whitney *U* test.

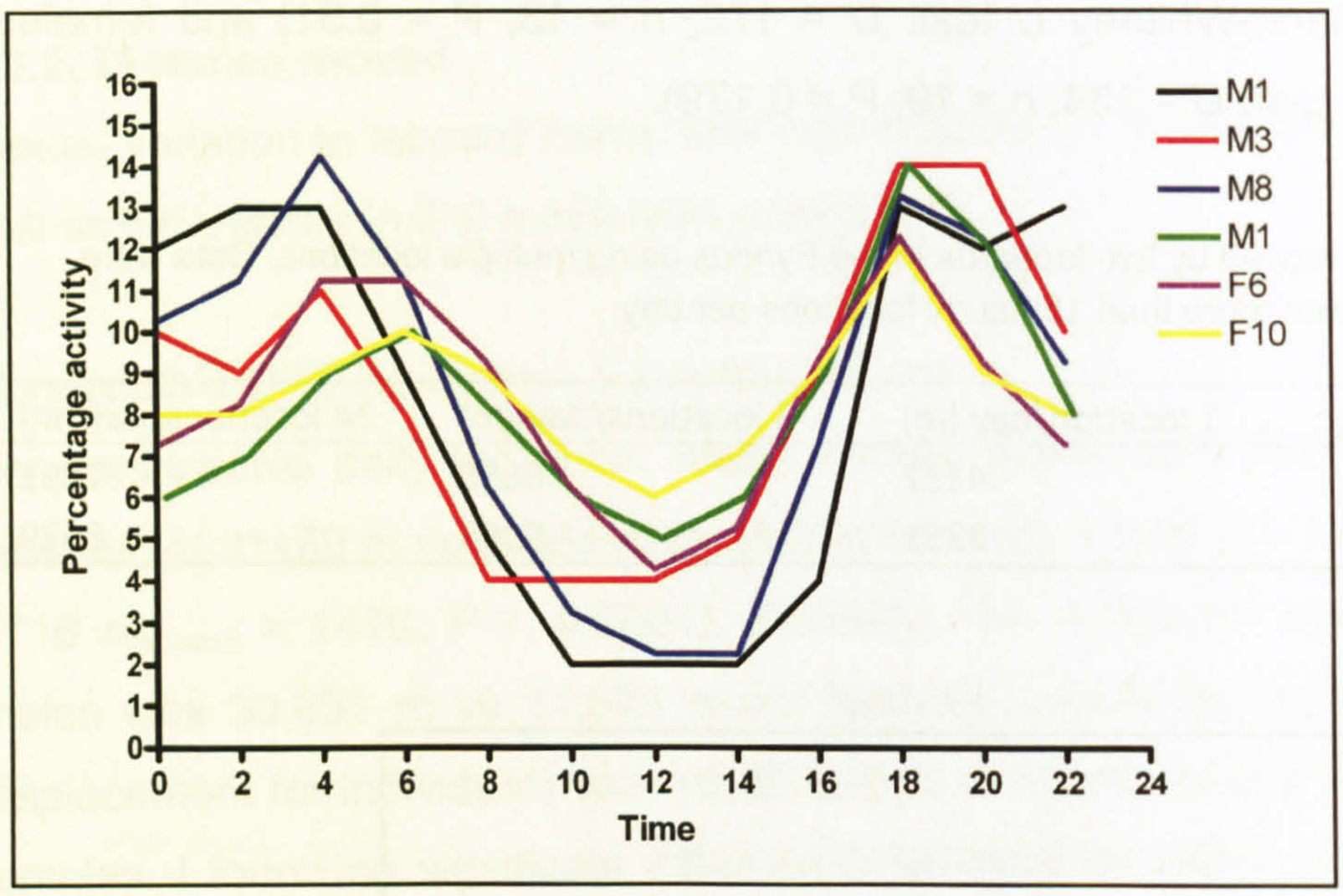


Figure 6.3. Percentage daily activity for six leopards using activity counts for the X-axis.

Day/night distance moved using ≥4 hr ≤ 8 hr locations

Observation of differences in day/night movement show that males were moving significantly further per 12 hours at night than during the day (Mann-Whitney *U* test: $U = 0$, $P = 0.001$), but not significantly further than females during the day (Mann-Whitney *U* test: $U = 7$, $P = 0.35$) or night (Mann-Whitney *U* test: $U = 6$, $P = 0.16$), whereas females move similar distances day and night (Table 6.3). Low sample sizes prohibited robust statistical analyses.

6.3.3. Activity as determined by collar sensors

Activity using GPS collar activity counts

In total I retrieved collar data for 4 males and 2 females, with a mean of 246±38 days and 68,542±10,074 activity recordings taken per animal. Activity counts were significantly different between individuals (X-axis, $P = 0.0015$; Y-axis, $P = 0004$). Comparing X and Y values for the same individuals resulted in no significant differences (Mann-Whitney *U* test: $U = 14$, $P = 0.589$). I then used the Activity programme supplied by Vectronics to graph data for a visual comparison to demonstrate whether data from the X-axis varied from that of the Y-axis. Figure 6.2 confirms they are similar to each other when comparing the same leopards, and so only the X-axis was used to compare the daily activity patterns across

seasons. This showed that leopards are predominantly nocturnal, with a drop in activity between 22.00 and 02.00 (Fig. 6.3). Seasonal differences in activity were not explored due to a lack of data.

6.3.4. Lunar effect on hunting efficacy

I identified 45 leopard kills that took place at night, of which 34 occurred at lower light conditions between new moon and half moon (Fig. 6.4). Of the remaining 11 kills, 5 occurred during a full moon, although 3 of these were when it was raining. Kills included in the analyses included 10 rock hyraxes (diurnally active), 8 klipspringers (diurnal), 1 grysbok (nocturnal), 1 oryx (diurnal), 1 grey duiker (diurnal/nocturnal), 1 porcupine (nocturnal) and 1 cow (diurnal). A camera trap photograph of a female leopard with a hyrax it had killed was taken on a dark night with a new moon (Fig. 6.5). The preceding photograph, taken 15 minutes earlier, showed her moving in the opposite direction towards an outcrop where hyraxes have been observed, suggesting the kill took place within the intervening 15 minutes.

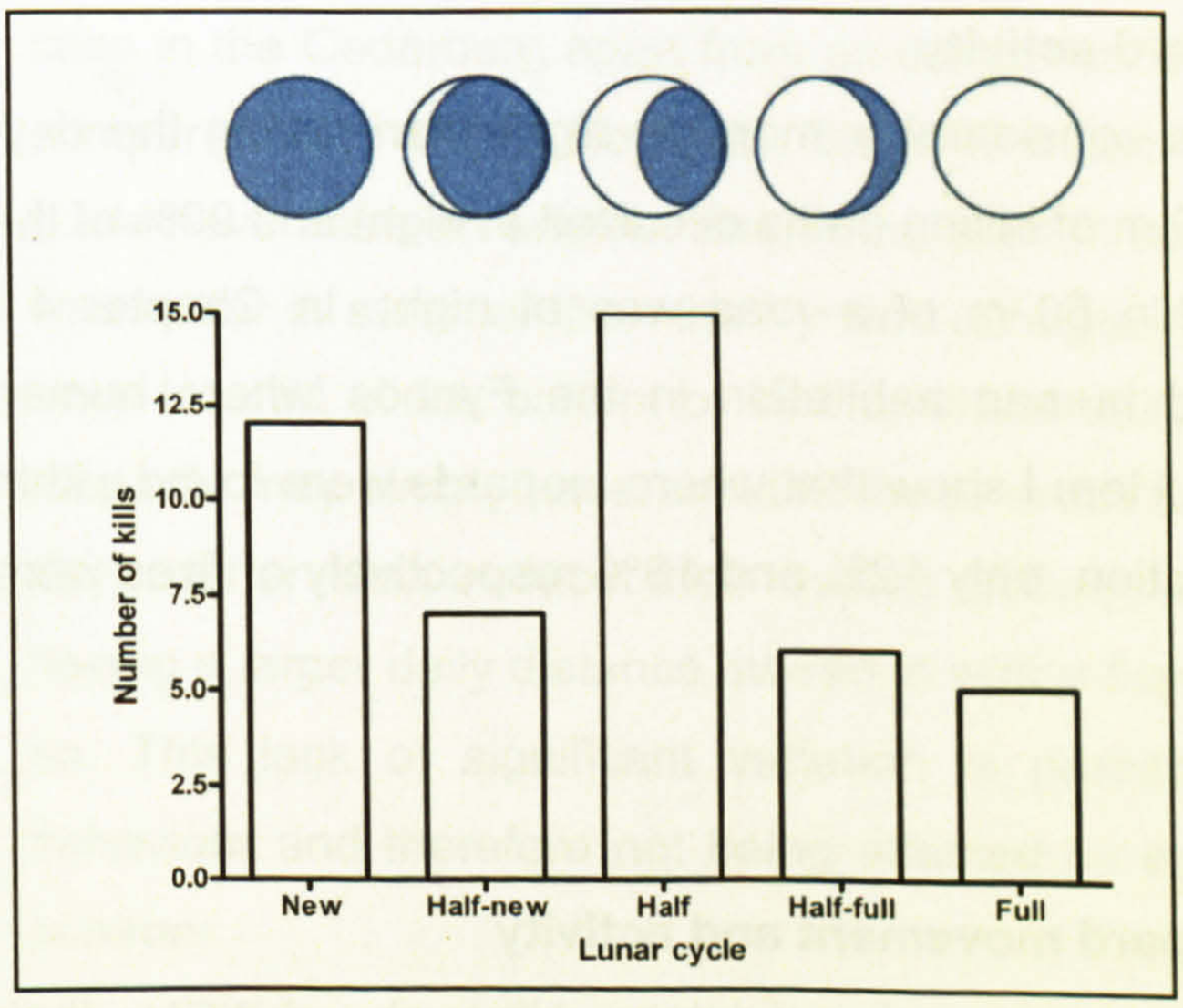


Figure 6.4. Number of kills made in relation to lunar cycle, where new moon is the darkest period, and full moon the brightest.

Figure 6.5. Female leopard with a rock hyrax killed between 02.22 and 02.37.

6.3.5. Human impact on leopard activity

Leopards used roads or paths considerably more at night than during the day. 84% of all GPS points within 25 m of hiking paths occurred at night and 90% of the time leopards were found within 50 m of a road was at night. In Chapter 4 I showed that leopards avoided human habitation in the Fynbos where human habitation was most prominent. Here I show that where leopards were found within 50 m or 100 m of human habitation, only 12% and 16% respectively of fixes were during the day.

6.4. Discussion

6.4.1. Factors influencing leopard movement and activity

Leopards are believed to be nocturnal predators although, due to their opportunistic hunting behaviour, diurnal activity does occur (Hamilton, 1976; Bailey, 1993; Stander & Hayden, 1997; Swanepoel, 2008). However, most studies in Africa have been done on leopards in savanna habitats. In forests and the mountains of the Western Cape, leopards have been recorded as being diurnal or

crepuscular (Norton & Henley, 1987; Jenny & Zuberbühler, 2005). These areas differ considerably, particularly in terms of competition with other predators and levels of human impact or influence, factors which often affect leopard behaviour. For instance, nocturnal behaviour has been associated with persecution by humans (Grimbreek, 1992). Where there is a preference for diurnal activity, it may be associated with competition with larger predators (Muckenhirn & Eisenberg, 1973; Azlan & Sharma, 2006). Larger predators no longer inhabit the Cederberg.

I showed that leopards in the Cederberg are nocturnal rather than diurnal, using a combination of camera trap results, GPS-collar movement and collar activity data to support these findings. Although camera traps have been used to study leopard behaviour elsewhere in Africa (Steyn, 2007; Balme *et al.*, 2010), none used cameras to determine leopard activity, although it has been used on tigers (Azlan & Sharma, 2006), jaguars (Maffei *et al.*, 2004), cougars (Monroy-Vilchis *et al.*, 2009), ocelots *Leopardus pardalis* (Di Betetti *et al.*, 2006) and leopards elsewhere in their range (Azlan & Sharma, 2006; Spalton *et al.*, 2006).

Savanna leopards differ from forest leopards in having no significant differences in seasonal behaviour (Bailey, 1993). The same appeared to be the case in the Cederberg apart from an insignificant lull in midday activity in summer compared with winter. However, this was based on camera trapping results and could have been an artefact due to the sites in which I set my cameras: the Karoo was hotter in summer than the Fynbos (Chapter 2), and 66% of my camera traps were located at the bottom of kloofs, where daily temperatures were higher. The leopards may simply have avoided these areas during the hotter parts of summer days rather than reduce their overall activity. Karoo males were recorded as having a larger daily distance moved in winter than in summer, but not significantly so. This lack of significant variation is probably attributed to their nocturnal behaviour and therefore not being affected by extreme day-time temperatures in summer.

Differences in daily movement or displacement were observed based on the number of GPS locations used per day. The differences between using 1 location/day and hourly locations resulted in the underestimation of female daily distance moved. So much so, that I observed no significant difference between

males and females when using 6 or 24 locations per day, suggesting that males were moving in a more linear fashion than females.

Using daily locations, the distances moved by Cederberg leopards were higher than the 1.7 km found by Bailey (1993), similar to the figures obtained by Hamilton (1976), Norton & Henley (1987) and Swanepoel (2008), but less than Bothma & le Riche (1984) and Grimbreek (1992). Considering the large home ranges in the Cederberg and the significant correlation between distance moved and home range size (Hamilton, 1976; Norton & Henley, 1987), I expected movement to be similar to leopards in the Kalahari (Bothma & le Riche, 1984). Karoo leopards with their large home ranges conformed to this principle, and moved further than Fynbos leopards.

The threat of persecution (see Chapter 1) can also alter leopard behaviour (Grimbreek, 1992). I found that, although leopards were more active at night near areas of human habitation, roads or paths, human activity was unlikely to have influenced leopard behaviour there was very little human activity and very few paths or roads in the Karoo, yet leopards were still predominantly nocturnal.

6.4.2. Intersexual variation in movement and activity

Females tended to be more active during the day than males, with diel activity patterns showing males moving significantly more and further during the night than day, as reported elsewhere (Stander, 1996). Odden & Wegge (2005) observed similar patterns, concluding that females avoided possible confrontation by being more active when males were not, and by avoiding the linear paths used by the males for their linear movements. A contributing factor to this behaviour could have been the small home ranges recorded by Odden & Wegge (2005). Home ranges in the Cederberg were considerably larger, resulting in minimal risk of leopards confronting one another. Differences in movement patterns and activity are, therefore, most likely due to differences in feeding behaviour as well as males covering larger distances to defend larger territories. Kure (2003), for instance, observed female leopards often backtracking and moving in an unpredictable manner while searching for food, while males used roads to patrol their territories.

6.4.3. Hunting strategies of Cederberg leopards

The diurnal activity of the main prey of leopards, as recorded in my camera trapping surveys, confirms Norton & Henley's (1987) observations. However, their suggestion that leopards were predominantly diurnal in the Cederberg because they were feeding on diurnal prey was not the case. Using both GPS location cluster analyses and photographic evidence from camera traps, it is clear that leopards are killing rock hyraxes and klipspringers at night. Figure 6.5 was one of several photographs of leopards investigating rocky outcrops in front of cameras where hyraxes were seen to be active in the day. There is little evidence to suggest the hyraxes are moving about at night, as the infra-red cameras would have recorded any such activity. Leopards must therefore have excavated these rock-dwelling animals.

However, it was unclear why leopards would hunt larger diurnal prey at night. Leopards have excellent night vision (Sunquist & Sunquist, 2002; Balme *et al.*, 2007), and so I examined hunting success or preferences for low light conditions by comparing lunar cycles to kills made. There was a tendency for leopards to make kills on darker nights, with only two kills on nights with a full moon and no cloud and/or rain. This supports the notion that leopards have an advantage hunting diurnal prey in rocky habitat where it is difficult to evade predation under low-light conditions. One of their main prey items, klipspringer, are vigilant towards predators during the day, standing on elevated positions with the males on sentry duty (Estes, 1992). They will often flee on hearing the alarm calls of other animals, mostly communal dwelling rock hyraxes. At night, hyraxes remain in rocky cracks and crevices and are therefore unable to detect predators. This may make it easier for leopards to hunt diurnal prey at night.

6.5. Conclusion

I have shown, using a combination of camera trapping and GPS radio-collar data, that leopards in the Cederberg are nocturnal predators feeding off diurnal prey at the darkest times of the month. Males, traversing the landscape in a more linear fashion than females, move significantly more at night than during the day; there were no seasonal differences in leopard movement. In the absence of large,

competing carnivores, leopards are active at the times that appear to enhance their hunting success, and are seemingly unaffected by anthropogenic influences.

CHAPTER 7

Diet determination of the Cape mountain leopards using GPS location clusters and scat analysis

This Chapter has been published as: Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. (2010). Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology*, doi:10.1111/j.1469-7998.2010.00757.x. (see Appendix 4).

Summary

Studying leopards in mountainous regions is challenging and there is little ecological information on their behaviour in these habitats. I used data from GPS radio-collared leopards in conjunction with leopard scat analysis to identify key aspects of leopard feeding habits in the Cederberg Mountains of South Africa. I located 53 leopard kill/feeding sites from clustered GPS locations of ≥4 hrs and analysed 93 leopard scats. Both methods showed that klipspringers and rock hyraxes were the most common prey. GPS location clusters showed that the time leopards spent at a given location was positively related both to the probability of detecting prey remains and to prey size. Leopards made significantly more large kills in winter than summer (P=0.003); there was no significant difference between male and female leopards in the average number of large kills or the average time spent at large kill sites. I show that, when studying large carnivores in inaccessible areas, it is important to use a combination of techniques to understand their feeding ecology and that GPS locations can be used to give an accurate measure of diet even when small prey are being taken.

7.1. Introduction

Leopards have the widest distribution of the large cats in Africa, yet their habits and feeding ecology outside savanna habitats are poorly understood (Norton *et al.*, 1986; Hart *et al.*, 1996; Henschel *et al.*, 2005; Jenny & Zuberbühler, 2005). Throughout their range they have a broad diet, feeding on mammals ranging in size from mice to eland weighing up to 900 kg, as well as birds, reptiles and fish (Hamilton, 1976; Norton *et al.*, 1986; Bailey, 1993). Typically, leopards appear to

take prey in proportion to their availability in a given area. In savannah, where medium- to large-sized ungulates predominate, most prey is in the 20 – 80 kg range (Hamilton, 1976; Bailey, 1993; Hayward *et al.*, 2006), whereas in African forested areas, where potential prey items are smaller, animals taken are in the 7 – 30 kg range (Hart *et al.* 1996; Ray & Sunquist, 2001; Henschel *et al.*, 2005). Where larger animals are not available, leopards commonly feed on small prey less than 20 kg (Grobler & Wilson, 1972; Bothma & Le Riche, 1984; Norton *et al.*, 1986; Ray & Sunquist, 2001; Henschel *et al.*, 2005). In the mountains of the Western Cape, South Africa, where leopards are half the mass of leopards elsewhere in southern Africa (Stuart, 1981; Norton & Lawson, 1985), small prey such as rock hyrax have been reported to form the majority of their diet (Norton *et al.*, 1986).

Leopard diet studies have typically used faecal analysis or direct observations in savanna or forest habitats (Grobler & Wilson, 1972; Bothma & Le Riche, 1984; Norton *et al.*, 1986; Le Roux & Skinner, 1989; Bailey, 1993; Kure, 1993; Bothma & Le Riche, 1994; Hart *et al.*, 1996; Henschel *et al.*, 2005). However, sightings of large predators such as leopards are rare in rugged and remote mountain areas and scats hard to locate, making studies of their feeding habits difficult. VHF telemetry has been used to study leopard ecology, but with limited success (Norton & Lawson, 1985; Norton *et. al.*, 1986; Bailey, 1993; Jackson, 1996). More recently, use of GPS radio collars has greatly enhanced our understanding of carnivore biology in remote areas through retrospective analysis of GPS location data (McCarthy *et al.*, 2005). Together with activity and home range information, GPS collars have been used to locate and identify kills made by large carnivores such as wolves (Sand *et al.*, 2005; Demma *et al.*, 2007; Zimmermann *et al.*, 2007; Webb *et al.*, 2008) and cougars (Anderson & Lindzey, 2003; Knopff *et al.*, 2009) by investigating cluster locations (consecutive GPS locations in close proximity to each other) over a period of several hours or days. Generally, however, larger kills are located, and the value of GPS locations for identifying sites of smaller kills remains unclear (Knopff *et al.*, 2009).

Here I have used faecal analysis in conjunction with analysis of GPS cluster locations to study leopard feeding habits in the Cederberg. My aims were to (i) determine the diet of leopards; (ii) test whether leopard kill or feeding sites could be located using clusters of GPS locations and determine the significance of the

time leopards spent at different feeding sites; (iii) see whether there were seasonal differences in male and female feeding patterns; and (iv) compare GPS cluster location analysis with leopard faecal analysis to determine whether this was a reliable indicator of leopard diet in an area where they were believed to take small prey.

7.2. Methods

7.2.1. Study area

See Chapter 2.

Mammals observed in leopard diet were referred to in Chapters 2, 5 and 6.

7.2.2. Leopard capture and immobilisation

See Chapter 3.

7.2.3. GPS collars and location cluster analyses

For collar information and schedules see Chapter 3.

GPS clusters identified were investigated between August 2008 and April 2009. Clusters of locations that could signify potential feeding sites were defined as 2 locations within 50 m radius or >2 locations within 100 m of each other over a minimum 4-hour period (Fig.7.1). I focussed my attention on more recent kills (<1 yr), but also investigated some older kills. Cluster analyses were conducted visually using the Arcview 3.2 Moose-on-a-Leash function. Once potential feeding sites were identified, GPS coordinates were programmed into a handheld Garmin eTrex Venture® Cx (Garmin International, Olathe, Kansas, U.S.A) and the central point in the tightest cluster examined on foot. A maximum of 30 minutes was spent searching for prey remains within a radius of 50 m of this point. Bones, hair, horns, feet and hooves were collected and used to identify prey species. Biomass consumed was calculated from the average mass of the prey item.

7.2.4. Seasonal and sex differences in leopard diet

GPS location clusters provided the minimum time at a kill. I was unable to investigate all potential kills, but because sites occupied by a leopard for ≥24 hrs were indicative of them having made a kill >10 kg (see Results), I analysed these potential kills made by individual leopards in both summer and winter over a four

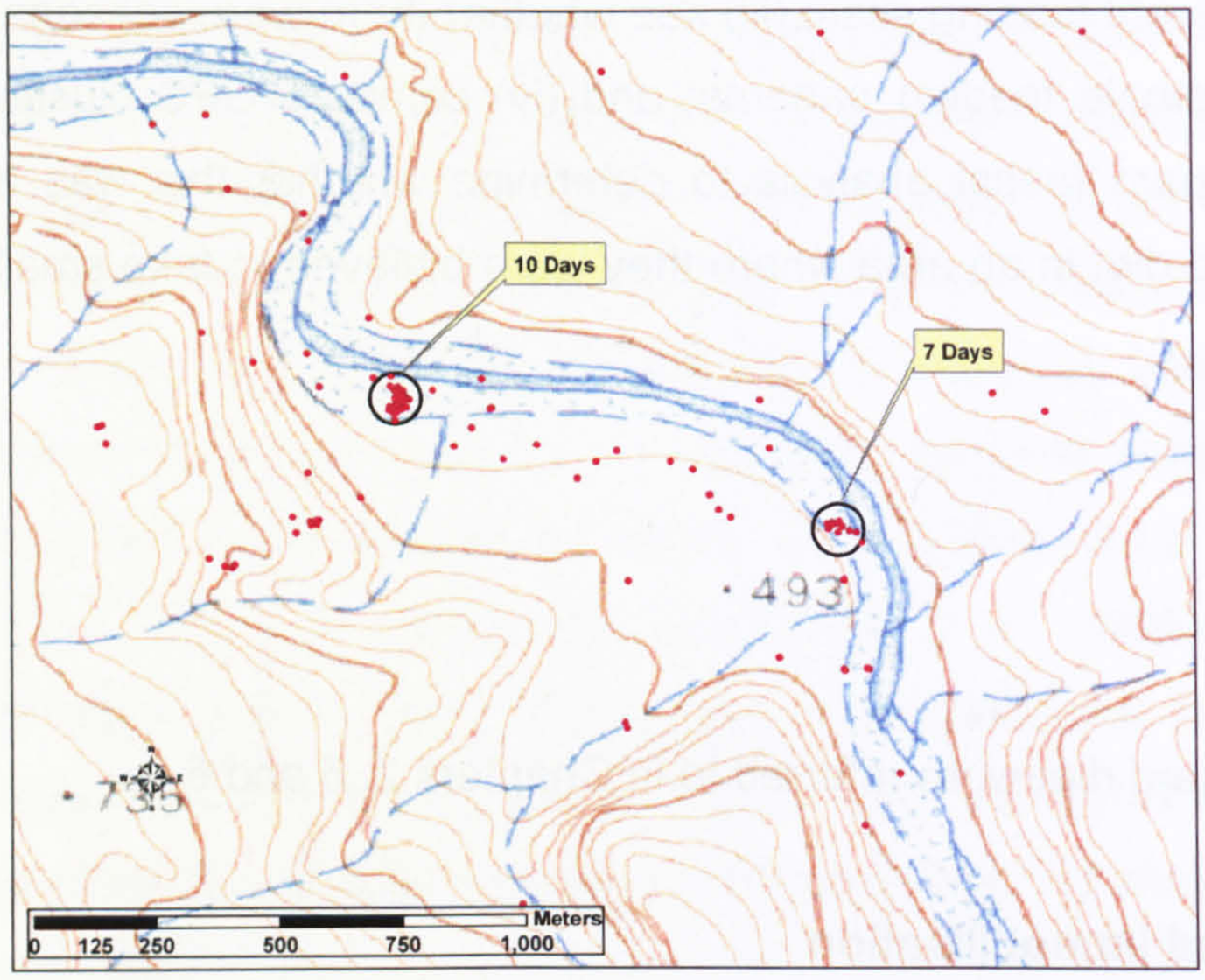


Figure 7.1. Topographical map showing a selection of GPS points (red circles) for leopard M2, including 2 clusters of points circled, one for 10 days, and one for 7 days. These signify large kills of mammals such as cows or donkeys. The proximity to the river suggests that after a flood, evidence of such kills would be washed away.

year period. Kill site analysis generated (a) the number of large kills and (b) the amount of time spent at these kills in both summer and winter. Seasonal and sexual differences were compared using two-tailed Mann-Whitney tests. Where data were not available for an individual in one season, means were used. A generalized linear model was used with the binomial distribution and a single trial and the logistic link function to model whether a kill was found or not in relation to three explanatory variables: time from kill to time of investigation, time spent at the kill and season. The allometric relationship was explored between time on kill and the estimated mass of the prey by modelling the logarithm of time on kill in relation to the logarithm of prey mass.

7.2.5. Faecal analysis

Leopard scats were collected opportunistically between 2004 and 2008 in both Fynbos and Karoo biomes. As successive samples were collected infrequently over such a long period, it was assumed that the same prey item was only represented in one individual scat. Scats were identified as belonging to leopards on one or more of the following criteria: (a) shape (Norton *et al.*, 1986), (b) scat diameter >20 mm (Norton *et al.*, 1986; Hart *et al.*, 1996; Khorozyan & Malkhasyan,

2002), (c) presence of leopard spoor or marking where the scat was collected and (d) the scat contained leopard hair ingested through interspecific killing or grooming (Ott, Kerley & Boshoff, 2007); scats <20 mm diameter were discarded unless leopard hair was present.

Dried scats were soaked in 4% formalin for 24 hours, washed over a 1.5 mm sieve, the hair separated from other remains, and oven-dried at 60°C (Norton *et al.*, 1986). Hair was cleaned in 96% alcohol and sulphuric ether mixture in equal measures (Keogh, 1979; 1983; 1985), washed in distilled water and left to dry.

Cuticular hair scale pattern was the main means to identify prey. Hair from each scat was evenly spread across a grid divided into forty-nine 25 cm^2 squares and an assortment of 5 hairs selected from random blocks. Hair scale imprints made using nail varnish (Ott *et al.*, 2007) were compared to photographs from a reference collection at the Centre for African Conservation Ecology (ACE), Nelson Mandela Metropolitan University (Ott *et al.*, 2007, Rautenbach, 2010), published photographs and keys, and samples from animal skins. Macroscopic features, such as hair length and colour aided identification, as did any remains of bone fragments, feet and hooves. Individual species that were not identifiable were grouped; e.g. 'lagomorphs' included Smith's red rock rabbit *Pronolagus ruprestris*, Cape hare *Lepus capensis* and scrub hare *Lepus saxatilis*. Smaller rodents were also difficult to identify to species level, although some were identified by teeth found in the scats (de Graaff, 1981). Birds and insects were classified to their order.

7.3. Results

7.3.1. Analysis of leopard diet using GPS location clusters

GPS data were collected from 10 adult leopards (7 males, 3 females) for periods ranging from 5 months (836 locations) to 18 months (3263 locations), (12.0±1.2 months, 1781±273 locations). The success rate at obtaining GPS locations was 75.8% (range 57.4%–87.3%) of the total number of locations programmed for download.

Of 101 GPS cluster locations identified and investigated as potential kill sites, 53 kills (52.5%) were located. The majority of prey items consisted of klipspringers (39.6%) and rock hyraxes (30.2%) (Table 7.1). Other small antelope (grey duiker and grey rhebok) made up a further 13.3% of kills and porcupines

Table 7.1. Leopard feeding remains located using clusters of GPS locations. Livestock consisted of a goat and a calf; only one lagomorph, a Smith's red rock rabbit, was found. Weight ranges were divided into <10kg, 10<20 kg and ≥20 kg; average weights derived from Skinner & Smithers (1990).

	No.	No. hours at kill site (range)	Weight range (kg)	Average weight (kg)	% of kills	% of total biomass
Lagomorph	1	4	0<10	1.6	1.9	0.2
Rock hyrax	16	4.0–24.0	0<10	3.8	30.2	6.6
Klipspringer	21	10.0–78.0	10<20	12.5	39.6	28.6
Grey duiker	4	24.0–48.0	10<20	19.7	7.6	8.6
Porcupine	5	10.0–28.0	10<20	17.5	9.4	9.5
Grey rhebok	3	34.0–52.0	≥20	21.0	5.7	6.9
Livestock	2	66.0–92.0	≥20	70.0	3.8	15.2
Gemsbok	1	90	≥20	225.0	1.9	24.5

9.4%. Based on average biomass, small antelope formed 44.1% of the diet, of which klipspringer was 28.6%, grey duiker 8.6% and grey rhebok 6.9%. Gemsbok (one) and livestock (goat and a calf) comprised 24.5% and 15.2% of the total biomass respectively. One juvenile leopard killed and eaten by an adult male leopard was not included due to difficulty in estimating time spent on the kill. Leopards consumed almost all of their prey for animals in the <25 kg class. Animal stomach contents were not eaten other than for small rodents, which leopards ate whole.

The successful location of animal remains correlated positively with the length of time the leopard had spent in the vicinity of the kill (Fig. 7.2). Successful location of a kill increased from 34.4% at sites occupied for <24 hrs to 83.8% for sites occupied for >24 hrs. Eighty-seven (86.1%) clusters investigated were <1 year old (Table 7.2). The generalized linear model to relate sex and time on kill to whether the kill was found showed that only time on kill was significant, viz. $\text{logit}(p) = -1.027 + 0.0593t$, where p is the probability of finding the kill and t is time on the kill. The SE of the estimated regression coefficient for t was 0.0152 ($t = 3.90$, $df = 99$, $P<0.001$). Backtransforming to probabilities, this suggests that the probability of finding the kill was 0.32 if t = 6 hrs, 0.39 if t = 10 hrs, and 0.73 if t = 34 hrs. These three values were the lower quartile, median and upper quartile of observed time on kill. The allometric relationship between the estimated mass of prey m (kg) and the time on kill t (hrs) was $t = 3.05\ m^{0.828}$; the SE of the exponent

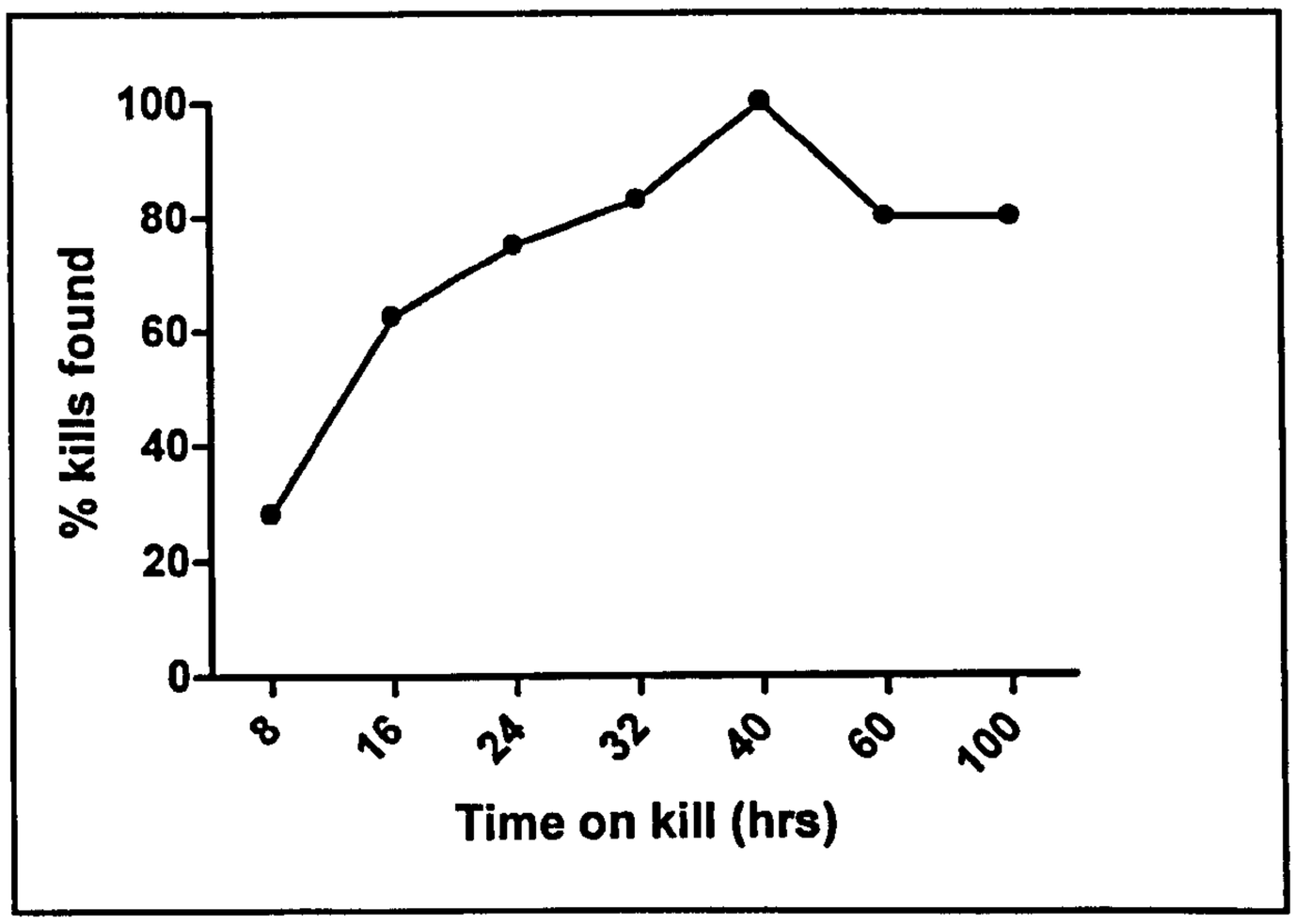


Figure 7.2. Proportion of kills found in relation to time a leopard spent in the vicinity of kill, based on GPS location clusters (n = 101).

Table 7.2. Percentage of GPS locations where a leopard spent less or more than 24 hours at which prey remains were found <1 year and >1 year later.

Locations investigated	<1 yr later	>1 yr later	All
<24 hrs	34.4 (n=61)	33.3 (n=3)	34.4
>24 hrs	92.3 (n=26)	63.6 (n=11)	83.8
Total	51.7 (n=87)	57.1 (n=14)	52.5

was 0.0969 ($t = 8.55$, $r^2 = 0.59$, $P<0.001$). Thus the mass of the prey accounted for 59% of time on the kill. The time interval between the kill and searching for it was not significant in predicting whether a kill was found regardless of how this variable was included in the set of explanatory variables.

7.3.2. Analysis of leopard scats

Scat analysis showed that klipspringer (44.1%) and rock hyrax (34.4%) were the most frequent prey items. Other species (Table 7.3) included aardwolf *Proteles cristatus,* small antelopes, lagomorphs, mongooses (3 species) and porcupine. Smaller species (<2 kg), such as mongooses, rodents and birds, were not found using GPS location clusters but were identified in 19/93 (20.4%) leopard scats. However, they only accounted for <1% of prey biomass (13.1/1430.8 kg). Species were present at comparable frequencies in both scats and at GPS-located kill sites for livestock (3.2% vs. 3.8%), rock hyrax (34.4% vs. 30.2%) and small antelopes

grouped (51.5% vs. 52.9%). Of these, klipspringer remains were found in 44.1% of scats and at 39.6% of GPS-located kills (Fig. 7.3) ($\chi^2 = 3.70$, df = 3, P = 0.295).

7.3.3. Predicting prey or prey mass from GPS location clusters

Animal remains recovered at potential kill sites revealed a positive correlation between time spent in the vicinity of the kill and estimated weight of the prey item (Fig. 7.4) (r = 0.857, n = 53, P<0.05). Of kills when the leopard spent <24 hrs in the vicinity, 72.7% represented prey species weighing less than 3.8 kg (n = 16). When time spent on a kill was >24 hrs, 96.7% (n = 30) were species weighing >10 kg, usually ungulates or porcupines.

7.3.4. Seasonal variation in leopard diet using GPS clusters

In total, 107 months of GPS activity were analysed in both summer and winter, and 232 predicted larger kills of ≥24 hrs were detected, amounting to a minimum of 12,092 hrs at larger kills (mean 50.02±18.05 hrs per kill). Using the average number of kills per season, leopards killed significantly more large prey in winter (mean 2.71±0.50 per month; n = 134) than summer (mean 1.77±0.58 per month; n=98) (P=0.003). Shown as a function of time, this equates to an average of 148.0±14.6 h/month in winter and 85.7±19.0 h/month in summer (P=0.015).

Table 7.3. Prey items recorded in leopard scats in the Cederberg Mountains (n=93).

Prey	Number of occurrences	Frequency of occurrence	% prey biomass
Klipspringer	41	44.1	35.8
Rock hyrax	32	34.4	8.5
Lagomorph	10	10.8	1.7
Small rodent	9	9.7	0.1
Grey rhebok	7	7.5	10.3
Mongoose	6	6.5	0.6
Baboon	4	4.3	6.4
Bird	4	4.3	0.2
Cape grysbok	3	3.2	2.2
Goat	3	3.2	23.7
Grey duiker	3	3.2	4.1
Aardwolf	2	2.2	1.2
Porcupine	2	2.2	2.4
Springbuck	1	1.1	2.7
Total	127	136.6	100.0

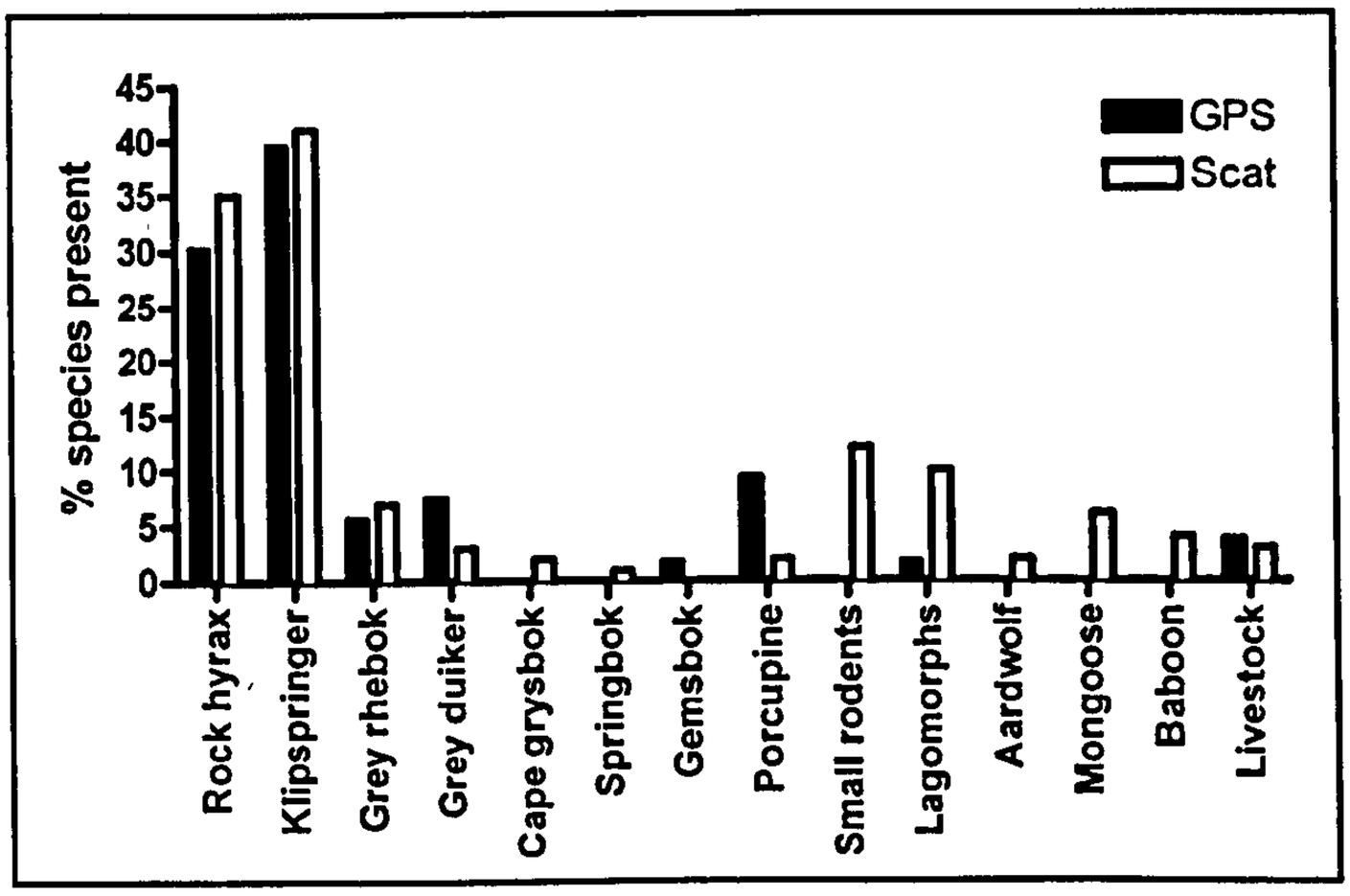


Figure 7.3. Comparison of species recorded in the diet of Cederberg leopards using scat analysis and GPS cluster locations.

However, for average number of large kills per month, there were no significant differences between male (2.35±0.19) and female (2.01±0.30) leopards (P=0.409), nor for average time on large kills (131.2±16.7 h vs. 83.5±18.8 h; P = 0.174).

7.4. Discussion

GPS location cluster analysis has previously been used to study the diet of cougars in North America and wolves in Scandinavia (Anderson & Lindzey, 2003; Sand *et al.*, 2005; Zimmermann *et al.*, 2007); both kill rates and the probability of a kill taking place, based on number of nights a predator spent at a site, were

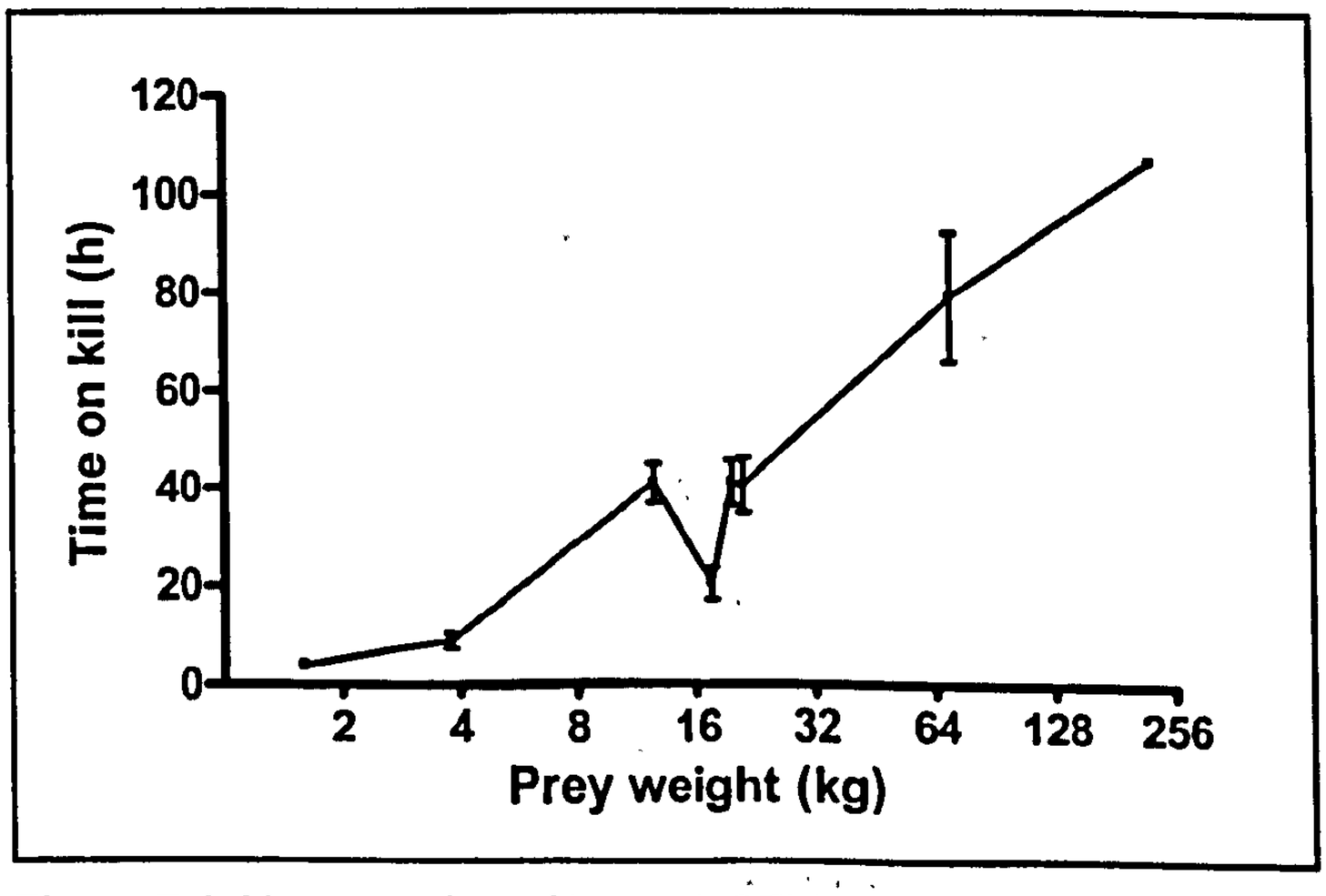


Figure 7.4. Mean number of hours (±SE) leopards spent in the vicinity of a kill compared with prey weight range (n=53, r=0.8571, P<0.01).

investigated. These were predominantly the remains of large prey. Here I have shown that GPS cluster locations can also be used to locate kills of a range of smaller prey items taken by a generalist predator and provide more detailed information on its feeding behaviour.

Twenty-three species were recorded in the diet of leopards in the Cederberg; similar diversity has been recorded in other studies (Hart *et al.*, 1996; Ray & Sunquist, 2001; Henschel *et al.*, 2005) and is indicative of the generalist feeding behaviour of Cape leopards. However, in terms of biomass consumed, nine species (small rodents, birds and insects) represented <1% of the total diet of leopards. Previous studies in the Cederberg reported the biomass of small ungulates and hyrax to be of equal importance in the diet (Norton *et al.*, 1986). I showed that small antelopes, in particular klipspringer, formed the greater part of the biomass consumed (scats = 57.7%; GPS = 44.1%) compared to rock hyrax (scats = 10.8%; GPS = 6.7%). Furthermore, whereas Norton *et al.* (1986) reported hyrax frequency in scats as 79.1%, I found this figure to be considerably lower (34.4%).

The prevalence of klipspringers and rock hyraxes in both scats and GPS data suggests a preference for leopards hunting in rugged, rocky terrain, the preferred habitat for these prey (Skinner & Smithers, 1990). This differs to studies in other parts of the Cape mountains, where leopards mostly preyed on grysbok, which prefer denser vegetation along rivers or lower slopes (Norton *et al.*, 1986; Skinner & Smithers, 1990). Small prey such as rodents (excluding porcupine) and birds could not be located from GPS cluster analysis; however, their importance in terms of biomass consumed was negligible. One insect was recorded but was not considered part of their diet, as it was most likely feeding on the scat. Thus scat and GPS techniques provided comparable results for identifying the most important prey of Cederberg leopards.

In rugged mountain areas where prey is small, predator kills are hard to locate without the assistance of GPS technology. In five years, only 18 confirmed leopard kills were opportunistically encountered (8 rock hyraxes, 6 antelopes, 3 livestock and 1 porcupine) without the aid of GPS, but in 9 months 53 of 101 potential kills were located by GPS cluster analysis. Kills were often hidden under bushes or rocky overhangs, unlikely to be found on an *ad hoc* basis, especially because leopards in the Cederberg Mountains consumed almost all of prey <25

kg. Remains would often only be part of a skull, hair and the rumen; because there were few scavengers in the area, kill remains could be located for up to 3.5 years. Finding kills using GPS clusters may not be as effective in areas where many scavengers are present, or where floods also affect the chances of finding kills.

The success rate at finding kills was a function of two measures of time; it was most likely to find the remains of kills <1 year old and where the leopard spent ≥24 hrs (92.3%). The success in locating a kill correlated positively to the length of time spent by the leopard at the kill site and prey mass. Kills where leopards fed on carcasses for ≥24 hrs consistently were prey weighing >10 kg. Large kills >40 kg were fed on for more than 66 hrs. The longest time spent at a location cluster was 184 hrs (Fig. 7.1), which was probably a large domestic animal. Since there was a low probability of locating kills at sites occupied for <24 hrs, these could have included resting as well as kill sites. More intensive GPS schedules may assist in refining the technique for finding smaller kills, although this may be prohibitively labour intensive (Knopff *et al.*, 2009).

Analysing GPS clusters also enabled the investigation of potential differences between male and female leopard feeding behaviour. No significant differences were found between the number of larger kills made by males and females, although this could be due to the low sample size. Logging kills using GPS clusters ≥24 hrs also provided temporal data on leopard feeding ecology: leopards made more larger kills per month in winter than summer. Historically, leopard depredation of livestock also occurred predominantly in winter (Stuart, 1981). GPS cluster analysis provides an important means of quantifying the impact of carnivore depredation on livestock. While remains of livestock eaten might be found from faecal analyses, any large animal fed on, such as a sheep or cow, had a high probability of detection using GPS cluster analyses. Using this technique, I located kills of a goat (66 hrs) as well as a 10 month old domestic calf (92 hrs). Kill sites occupied for >100 hrs were most likely cows, donkeys or, where present, large game. Thus GPS cluster analysis can be used as an interactive means to find livestock kills and minimise conflict with livestock farmers by identifying high risk areas and/or habitats.

7.5. Conclusion

This study demonstrated that the natural prey of leopards in the Cederberg Mountains consisted mainly of small- to medium-sized mammals weighing <20 kg, and that livestock and small prey such as rodents were an insignificant part of their diet. I found that feeding sites occupied for ≥24 hrs could be accurately detected by GPS analysis and that the time spent at prey sites correlated positively with prey size. Thus retrospective GPS analysis of predator movements in the Cederberg Mountains provided an accurate demonstration of leopard dietary habits and is a valuable tool for studying the feeding ecology of elusive carnivores that take a wide range of prey species and sizes.

CHAPTER 8
Conclusion

I sought to obtain key ecological data necessary to understand the conservation needs and role of leopards in the Cederberg Mountains, where they are the only surviving large predator. Leopards have persisted despite 350 years of persecution and loss of habitat. In particular, my aims were to address issues on range size, population density, movement and activity, as well as dietary preferences, to provide a basis for their future conservation.

8.1. Problems of studying leopards in a mountainous habitat

Direct observations of leopards in the Cape are so rare that remote data collection was the only way to study their behaviour and movements. GPS radio-collars enabled me to make observations on leopards using the GPS component on the remote-downloading collars to get a real-time location. Even so, these sightings were infrequent and mostly occurred at considerable distances (>100 m), so I could not use this approach to collect behavioural data. Furthermore, as soon as a leopard became aware of my presence, it moved off or hid in a rocky crack.

Collars had both GPS and VHF tracking functions. It was necessary first to track an animal with VHF, get a good idea of its location, and then use the UHF remote-download unit to access GPS information. However, tracking leopards using VHF telemetry in these rugged mountains proved very challenging. Signal reflections resulted in considerable effort having to be made to obtain a true bearing on the animal. This applied to both VHF and UHF radio signals. On one occasion, using the UHF downloading unit to recover collar data, I obtained data showing the leopard's position was 15 km away at right angles to the direction I was aiming the antenna, suggesting the signal was bouncing off a high cliff in the distance. As a result, VHF data collected in similar environments should be viewed with caution. Unless an animal is tracked with a high degree of accuracy, location data may be skewed, potentially significantly.

GPS data showed that 3 months tracking with a minimum of 6 locations per day would provide a good indication of leopard home range and movement parameters for that season. Currently available GPS radio-collars make it possible

to boost the recruitment of data to 12 locations per day for two 3-month seasons (*c.* 2000 locations) using a 1-C-cell GPS collar suitable for a leopard in the Cederberg. More refined location data could improve leopard diet determination using GPS location clusters. However, extreme environments increase chances of equipment failure. I had several collar failures and poor collar performance which affected my results.

Camera trapping gave me my first tangible evidence of leopards in the Cederberg. Although the infra-red film cameras I used to generate a population estimate were very useful, modern digital cameras with their much greater data storage capacity greatly facilitate data collection in remote areas. Because film cameras can only capture a maximum of 36 exposures, requiring extensive monitoring over adverse terrain, my camera trapping study was limited to the Karoo biome where little human activity occurred. More recently, digital cameras have been deployed successfully in the Fynbos, despite capturing countless photographs of hikers. A repeat of my camera trapping survey is planned for both Karoo and Fynbos biomes.

Documenting prey species and conducting a thorough prey density survey proved challenging and I was only able to obtain an estimate of relative prey abundance in the Cederberg, despite exploring several methods to quantify prey abundance. Thus Cybertracker™ data capture did not prove useful: aside from the technical issues, animals were either too scarce or too cryptic to collect enough sightings. I then investigated the possibility of using aerial thermal imagery to photograph and count prey. Species as small as hyraxes can be detected from up to 500 m and fine-scale thermal imaging can produce sufficient contrast between species, based on insulative properties of their fur, to aid identification (Boonstra *et al.*, 1994; Garner *et al.*, 1995; Gill *et al.*, 1997; McCafferty, 2007). I was unable to do this in the time-frame of my PhD but another PhD project will create a survey methods handbook for prey density surveys in the Cape mountains.

A great deal of my time was spent setting and checking traps, and so during the course of my study I refined the leopard capture techniques both to reduce the time spent monitoring the traps and to reduce injuries to any animals that were captured. A number of changes were made to the cages in an attempt to improve the safety for both leopards as well as by-catch such as klipspringers. A third inner door operating with a counter-weight was added; this closed after the animal was

caught, thereby limiting movement in the cage, and reducing capture injuries (Appendix 2). Trap transmitters were used to reduce the time taken to monitor the traps. Further innovations currently being tested include a remote Iridium satellite system which, with the use of a camera, would send regular photographs of the inside of the trap via satellite, to the base station several hours hike/drive away. These photographs are a safety precaution confirming the trap was not triggered. A photograph would also be taken on the trap being triggered and the doors dropping, obtaining an image of the trapped animal. This will reduce the time a leopard is in the trap. Also, a remote release mechanism, powered by a 12 V lead-acid battery, will enable the trap doors to be opened from the base, so that non-target species can be released quickly. With the development of the Iridium transmitter system for better monitoring purposes, I am also considering the use of foot-snare traps for the first time, since these are the most suitable trapping technique for large cats (Frank *et al.*, 2003). Previously, with such a remote area it was not possible to check foot snares frequently enough, particularly since capture rates will be low.

8.2. Have leopard densities changed in the last 30 years?

The home ranges of leopards in the Cederberg were significantly larger than previously recorded here, and as large as the largest recorded for the species across its range. This is probably due to the low productivity of the area and the habitat preferences of the leopards. There are several possible reasons why my home ranges were so much larger than those recorded previously by Norton & Henley (1987):

- VHF telemetry as used by Norton provides little more than minimum home range estimates in mountainous terrain where tracking is difficult (McCarthy *et al.*, 2005);
- The decline in key prey species, such as hyraxes, could have led to an increase in leopard home ranges. During the 1980s, when Norton & Henley (1987) studied leopards in the Cederberg, hyraxes were abundant and even considered a pest by farmers. During my study, although common, there were far fewer hyraxes. To investigate why, I initiated a study which showed a hyrax-specific form of tuberculosis in Cape hyraxes (Parsons *et al.*, 2008).

This pathogen may not directly cause the death of hyraxes, but may lower their immune system to a point that could affect their health and as a result natural survival. This may account for the cyclical fluctuations observed for the species (Skinner & Smithers, 1990). The 'dassie bacillus' *Mycobacterium tuberculosis* complex is not transferable to other species, so cannot affect the health of a predator through ingestion of an infected individual.

- Before my study, leopards were killed on a regular basis due to conflict with farmers. For example, between 1988 and 1990, 21 leopards were killed in the Cederberg, based on permits issued by Cape Nature. This does not include any illegal killing. The constant disruption in the system due to these removals may have affected the movements and resulting home ranges as determined by Norton & Henley (1987). The influence of my study and the establishment of the Cape Leopard Trust resulted in only 2 leopards being killed in 6 years, and so I was monitoring a more stable population. Little is known about the effects on movement as a consequence of disruptions, but it is possible it could have affected home range size.

Leopard densities have been shown to be lower in unprotected than protected areas (Balme *et al.*, 2010). In the Cederberg, protected areas were either too small or shaped in a way that resulted in leopard ranges overlapping with different land uses. Therefore, densities were dependent on the degree of protection afforded to leopards beyond the boundaries of these reserves. Taking into account the negative effects of high mortality rates on leopard populations, such as low breeding success, high cub mortality and low recruitment, population trends may have changed considerably since Norton & Henley (1987). It is possible that higher prey densities at that time resulted in higher leopard densities than at present and that the current stability of the leopard population and fewer key prey such as hyraxes, means that the low densities I recorded in the Cederberg are an optimal figure for the prevailing conditions.

8.3. Conservation of Cape leopards – small cats with big problems

My research has provided valuable insight into the ecology of a little-known and persecuted predator living in a human-influenced landscape. The initiation of my

research led me to establish the Cape Leopard Trust. The conservation benefits of the project were observed through a significant decrease in leopard mortalities in and around the study area. Furthermore, my research results were used to alter perceptions and management by farmers, and to inform the management of the species by the statutory conservation body, Cape Nature. As a result the following changes have occurred:-

- In March 2007, the Cederberg Conservancy, a 1700 km^2 area of private land managed in partnership with Cape Nature, formally committed to banning the killing or removal of leopards.
- The abandonment of relocation of so-called 'problem animals'. This was a common management practice in the past. I used two arguments to convince the authorities that this practice has no validity and may have adverse effects on the stability of the existing population. Based on the behaviour I recorded, relocations may have more negative ramifications than simply removing the 'offending' leopard. Evidence for this could be seen when a 'new' leopard took over a vacant territory, after a dominant animal died, and the resulting cub mortality caused by the new immigrant. Furthermore, differences in weight between Cape mountain leopards and leopards elsewhere in Africa led to a genetic study on the species. We have been able to confirm that sufficient genetic differences occur between this population and others so as to ensure relocation between populations is prohibited (Martins, 2006; A. Ropiquet *et al.*, unpubl. data).
- Another practice which I assisted in changing was the issuing of destruction permits of leopards by Cape Nature. Previously, permits were valid for 31 days, allowing landowners to set a trap for the full duration in an attempt to capture and kill a leopard. I raised concerns that the length of time allowed for the capture could result in another leopard being caught, as the 'culprit' would not remain in the area for this length of time. Permits are now only valid for 7 days.
- I used the results from my home range data to convince authorities and landowners that the removal of a dominant leopard was ill advised and not a solution to the problem, as the vacant territory would soon be filled by a new, immigrant leopard, which would not solve the problem.

- Although not yet part of provincial legislation, I have ensured that the draft leopard management policy formulated by Cape Nature states that, for a permit to be issued, the onus is on the landowner to show that in the event of a leopard depredation event, sufficient precautions had been taken by the farmer to protect the livestock. Were those precautions not in place, the farmer would have no legitimate recourse to destroy the animal in question.

The biggest known threat to leopards in the Western Cape is loss of habitat and persecution by farmers. Trophy hunting here is illegal, thus eliminating it as a threat. Potential leopard habitat in the Western Cape, excluding isolated areas where they have been sighted, is approximately 40,000 km^2. Conserved areas, state land and mountain catchment areas, recognised as prime leopard habitat, amount to about 10,000 km^2, one quarter of the demarcated area (Fig. 1.3). The other 30,000 km^2 accommodates a resident leopard population, but is privately owned land with crop and livestock farming and small towns: these cause considerable fragmentation of the habitat. Livestock farming increases the risk of leopard persecution due to conflict. Low lying hills and open areas may limit leopard movement or dispersal while, more recently, tourism activities have resulted in more land being converted to nature or 'game' reserves. Ironically, predators are not always welcome here due to the value of game animals which can be predated.

Given the low density estimates observed for two distinct biomes in the Cederberg Mountains where a population has been maintained without threat of persecution, concern needs to be raised for the remaining population in the Western Cape. A more detailed assessment of the available habitat and possible corridors linking these is needed to determine the actual size and security of this population.

8.4. Trophic cascades and restoring the Cederberg ecosystem

In the Western Cape, leopards are the apex terrestrial predator after lions and hyaenas were made extinct several hundred years ago. Their range has been reduced dramatically, and they now exist solely in the more rugged mountain regions where natural prey can still be found (Norton, 1986) and few people live. Understanding the role of leopards in the ecosystem as well as the importance of

conserving them is impossible without consideration of their distribution and the differences between the habitats in which they occur, namely the Karoo and Fynbos biomes.

For its size, the Fynbos has the highest recorded floral species density in the world (Bond & Goldblatt, 1984). Despite this plethora of plant species, the Fynbos has some of the lowest soil nutrient levels in the world (Johnson, 1992; W. Bond, pers. comm., 20/10/2010). As a result of low leaf nitrogen levels, limited numbers of herbivores prevail, contrasting significantly with the surrounding low lying regions where more palatable grass was present, and herbivores were abundant until changes in land-use and eradication by European settlers over the past 350 years (Johnson, 1992; Roche, 2008). The Fynbos mountains can now be viewed as islands in a sea of perturbed lowlands, and characteristics of this system need to be viewed in context, whether it be for plant or animal conservation (Boshoff *et al.*, 2003).

Although leopards no longer occur in parts of their Fynbos range, much of their mountain habitat remains intact. Apart from the near extinction of the charismatic cedar tree in the Cederberg, the mountain Fynbos would have remained largely unaltered over the past few hundred years. Significant habitat loss has occurred mainly in the lower lying regions where lions, hyaenas, and accompanying prey species suffered at the hand of human interventions. These areas, whether transformed by agriculture or not, are no longer suitable for the reintroduction of extirpated species. The perturbations resulting in large-scale fragmentation of the landscape, combined with human settlement and the unlikely event of people co-existing with these large predators and megafauna, mean that this loss of biodiversity is unrecoverable.

Threat or loss of current Fynbos habitat suitable for leopards is, however, a major concern for biodiversity conservation. Leopards, and the black eagle *Aquilla verreauxii*, are the main predators of rock hyraxes and klipspringers, the key prey species occurring in the mountain Fynbos habitat (Boshoff 1991). Hyraxes are group-living species which may impact severely on the reproduction of native plants (MacDonald, 1989). Left unchecked by predators, they could have a profound impact on the diversity of the Fynbos ecosystem, more so than their meso-predator counterparts. My observation of caracal and jackal movement in the Cederberg suggests there is little chance of a meso-predator release in the

rocky mountain parts of the Fynbos, as they appear to avoid these areas (Q. Martins, unpubl. data). Thus, in the Fynbos, there appears no need to reconstruct a historical predator guild, or reintroduce lost ungulate species. Instead, existing habitat needs to be conserved and corridors created to ensure safe passage for far ranging animals such as leopards to move between Fynbos islands.

The more arid Karoo, on the other hand, is a productive system for ungulates, and so would have been suitable for a broader assemblage of large predators. These have been extirpated, while leopards have also been eradicated over a vast part of their former range in the Karoo. Massive herds of springbok displayed nomadic behaviour, moving to where conditions were best. By 1897, the last of these large herds of antelope disappeared, mainly due to anthropogenic factors such as hunting, livestock farming, fencing and human habitation. Today the majority of the Karoo is severely degraded and humans have attempted to manipulate a system in constant flux by creating artificial water points for living and farming (Roche, 2008).

Because the Karoo differs between east and west, leopard and prey movement and behaviour differs. Little information exists for leopards occurring in the thickets of the Karoo in the eastern summer-rainfall area. I have as a result initiated a leopard PhD project as a comparative study with mine. In the Cederberg Succulent Karoo, a dry winter-rainfall area, leopards occur in very low densities, requiring large areas to exist. The open 'unsuitable' habitat in the Karoo results in leopard ranges being larger than in the Fynbos. Covering such vast distances increases the likelihood of leopards encountering other smaller predators, and on one occasion I found a caracal killed by a leopard. The influence of leopards on meso-predators in the Karoo where they co-exist may be significant. Thus removal of leopards from parts of their former distribution may be the reason for current conflict between farmers and caracals and jackals (Q. Martins, unpubl. data).

Although reconstruction of the historical predator guild and reintroduction of mega-herbivores would be ideal in order to maintain a functioning ecosystem (Ripple & Beschta, 2004, 2008; Beschta & Ripple, 2009), this could not include many of the low lying areas in the Western Cape. For instance, the wheat producing areas replaced a productive Renosterveld grassland system, which has been altered beyond repair. The Karoo, historically a highly productive system but currently degraded, has the potential to re-establish a functioning natural

ecosystem. Considering the vast perturbations caused by overgrazing by livestock, fences, human habitation and hunting, it is essential that conservationists consider the possibility of reintroducing a naturally occurring, but locally extinct faunal assemblage, and remove the fences that act as a barrier for animal movement through this fluctuating ecosystem.

8.5. Conclusions

I have addressed fundamental ecological questions about the leopards in the Cederberg Mountains where a paucity of information existed before. This has provided the foundation for an effective conservation management plan. The introduction of a 'no-hunt' policy in the Cederberg Conservancy has clearly shown the value of using leopards as an 'umbrella species' to aid the broader conservation of a unique and threatened environment. My data have been essential when convincing land-owners and conservation authorities about the need for effective conservation strategies. Data on population densities, movements, activity patterns, diet and habitat use of leopards in the Cederberg can now be used to investigate additional conservation measures such as the creation of suitable corridors for more effective leopard dispersal. I intend a long-term study which will monitor leopard numbers in the Cederberg, how they interact with meso-predators, and obtain a better understanding of their prey populations. Furthermore, I am coordinating research in other parts of the Western and Northern Cape to compare leopard and prey populations in different habitats, and establish ways of ensuring proper ecosystem functioning by reintroducing extinct fauna where it is practically possible and likely to have a positive impact.

References

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993). Compositional analyses of habitat use from animal radio-tracking data. *Ecology*, 74, 1313-1325.

Allen, J.R.M., Hickler, T., Singarayer, J.S., Sykes, M.T., Valdes, P.J., & Huntley, B. (2010). Last glacial vegetation of northern Eurasia. *Quaternary Science Reviews*, 29, 2604-2618.

Anderson, C.R. & Lindzey, F.G. (2003). Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management*, 67, 307-316.

Athreya, V. (2006). Is relocation a viable management option for unwanted animals – the case of the leopard in India. *Conservation and Society*, 4, 419-423.

Azlan, J.M. & Sharma, D.S.K. (2006). The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. *Oryx*, 40, 36-41.

Bailey, T.N. (1993). *The African leopard: ecology and behavior of a solitary felid.* Columbia University Press, New York, U.S.A.

Balme, G.A., Hunter, L.T.B. & Slotow, R. (2007). Feeding habitat selection by hunting leopards in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*, 74, 589–598.

Balme, G.A., Hunter, L.T.B. & Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, 73, 433-441.

Balme, G.A., Slotow, R. & Hunter, L.T.B. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, 13, 1-9.

Bellemain, E., Swenson, J.E., Tallmon, D., Brunberg, S. & Taberlet, P. (2005). Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. *Conservation Biology*, 19, 150-161.

Benson, J.F., Chamberlain, M.J. & Leopold, B.D. (2006). Regulation of space use in a solitary felid: population density or prey availability? *Animal Behaviour*, 71, 685-693.

Bertram, B.C.R. (1982). Leopard ecology as studied by radio tracking. *Symposia of the Zoological* Society *of London*, 49, 341-352.

Beschta, R.L. & Ripple, W.J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, 142, 2401-2414.

Beyer, H.L. (2004). Hawth's analysis tools for ArcGIS. http://www.spatialecology.com

Boardman, J., Foster, I., Rowntree, K., Mighall, T. & Gates, J. (2010). Environmental stress and landscape recovery in a semi-arid area, the Karoo, South Africa. *British Geographical Journal*, 126, 64-75.

Bond, P. & Goldblatt, P. (1984). Plants of the Cape flora: a descriptive catalogue. *Journal of South African Botany Supplement*, 13, 1-455.

Boonstra, R., Krebs, C.J., Boutin, S. & Eadie, J.M. (1994). Finding mammals using infra-red thermal imaging. *Journal of Mammalogy*, 75, 1063-1068.

Boshoff, A.F., Palmer, N.G., Avery, G., Davies, R.A.G & Jarvis, M.J.F. (1991). Biogeographical and topographical variation in the prey of the black eagle in the Cape Province, South Africa. *Ostrich*, 62, 59-72.

Bothma, J. du P., Knight, M.H., le Riche, E.A.N. & van Hensbergen, H.J. (1997). Range size of southern Kalahari leopards. *South African Journal of Wildlife Research*, 27, 94-99.

Bothma, J. du P. & le Riche, E.A.N. (1984). Aspects of the ecology and the behaviour of the leopard *Panthera pardus* in the Kalahari Desert. *Koedoe* (Suppl.) 27, 259-279.

Bothma, J. du P. & le Riche, E.A.N. (1994). Scat analysis and aspects of defecation in northern Cape leopards. *South African Journal of Wildlife Research*, 24, 21-25.

Broomhall, L.S., Mills, M.G.L., & du Toit, J.T. (2003). Home range and habitat use by cheetahs *(*Acinonyx jubatus*)* in the Kruger National Park. *Journal of Zoology*, 261, 119-128.

Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24, 346-352.

Cavalcanti, S.M.C. & Gese, E.M. (2009). Spatial ecology and social interactions of jaguars *(*Panthera onca*)* in the southern Pantanal, Brazil. *Journal of Mammalogy*, 90, 935-945.

Cobb, S. (1981). The leopard – problems of an overabundant, threatened, terrestrial carnivore. In: Jewell, P.A. & Holt, S. (ed.) *Problems in management*

of locally abundant wild mammals, pp. 181-192. Academic Press, New York, U.S.A.

Compton, J.S. 2004. *The Rocks & Mountains of Cape Town*. Double Storey Books (Juta & Co.), Cape Town, S.A.

Cowling, R. & Richardson, D. (1995). *Fynbos: South Africa's unique floral kingdom,* Struik, Cape Town, S.A.

Creel, S., Sprong, G. & Creel, N.M. (2001). Interspecific competition and the population biology of extinction-prone carnivores. In: Gittleman, J.L., Funk, S.M., Macdonald, D.W. & Wayne, R.K. (eds) *Carnivore conservation,* pp. 35-60. Cambridge University Press, Cambridge, U.K.

Creel, S., Spong, G., Sands, J.L., Rotella, J., Zeigle, J., Joe, L., Murphy, K.M. & Smith D. (2003). Population size estimation in Yellowstone wolves with error-prone noninvasive microsatellite genotypes. *Molecular Ecology*, 12, 2003-2009.

Daly, B., Power, J., Camacho, G., Traylor-Holzer, K., Barber, S., Catterall, S., Fletcher, P., Martins, Q., Martins, N., Owen, C., Thal, T. & Friedmann, Y. (eds). (2005). *Leopard (*Panthera pardus*) PHVA. Workshop report.* Conservation Breeding Specialist Group (SSC / IUCN) / CBSG South Africa. Endangered Wildlife Trust, Johannesburg, S.A.

Deacon, J. (1998). *Some views on rock paintings in the Cederberg.* National Monuments Council, Cape Town, S.A.

De Azevedo, F.C.C. & Murray, D.L. (2007). Spatial organization and food habits of jaguars *(*Panthera onca*)* in a floodplain forest. *Biological Conservation*, 137, 391-402.

de Graaff, G. (1981). *The rodents of southern Africa: notes on their identification, distribution, ecology and taxonomy*. Butterworth & Co, Durban, S.A.

Demma, D.J., Barber-Meyer, S.M. & Mech, L.D. (2007). Testing global positioning system telemetry to study wolf predation on deer fawns. *Journal of Wildlife Management*, 71, 2767-2775.

Di Betetti, M.S., Paviolo, A. & De Angelo, C. (2006). Density, habitat use and activity patterns of ocelots *(*Leopardus pardalis*)* in the Atlantic forest of Misiones, Argentina. *Journal of Zoology*, 270, 153-163.

Dillon, A. & Kelly, M.J. (2007). Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx*, 41, 469-477.

References

Dillon, A. & Kelly, M.J. (2008). Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. *Journal of Zoology*, 275, 391-398.

Donlan, J., Berger, J., Bock, C.E., Bock, J.H., Burney, D.A., Estes, J.A., Foreman, D., Martin, P.S., Roemer, G.W., Smith, F.A., Soule, M.E. and Greene, H.W. (2005). Re-wilding North America. *Nature*, 436, 913-914.

Elton, C. (1927). *Animal ecology*. Sidgwick and Jackson, London, U.K.

Estes, R.D. (1992). *The behaviour guide to African Mammals*. University of California Press, Berkeley, U.S.A.

Estes, J.A., Crooks, K., & Holt, R. (2001). Ecological role of predators. In: Levin, S. (ed.) *Encyclopedia of Biodiversity*, vol. 4, pp. 857-878. Academic Press, San Diego, U.S.A.

Frank, L., Simpson, D. & Woodroffe, R. (2003). Foot snares: an effective method for capturing African lions. *Wildlife Society Bulletin*, 31, 309-314.

Gannon, W.L., Sikes, R.S., and the Animal Care and Use Committee of the American Society of Mammalogists (2007). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 88, 809-823.

Garner, D.L., Underwood, H.B. & Porter, W.F. (1995). Use of modern infrared thermography for wildlife population surveys. *Environmental Management*, 19, 233-238.

Gervasi, V., Brunberg, S. & Svenson, J.E. (2006). An individual-based method to measure animal activity levels: a test on brown bears. *Wildlife Society Bulletin*, 34, 1314-1319.

Gill, R.M.A., Thomas, M.L. & Stocker, D. (1997). The use of portable thermal imaging for estimating deer population density in forest habitats. *Journal of Applied Ecology*, 34, 1273-1286.

Gittleman, J.L. & Harvey, P.H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10, 57-63.

Griffiths, C.J. & Harris, S. (2010). Prevention of secondary extinctions through taxon substitution. *Conservation Biology*, 24, 645-646.

Grimbreek, A.M. (1992). *The ecology of the leopard (*Panthera pardus*) in the Waterberg*. MSc thesis, University of Pretoria, Pretoria, S.A.

Grobler, J.H. & Wilson, V.J. (1972). Food of the leopard *Panthera pardus* (Linn.) in the Rhodes Matopos National Park, Rhodesia, as determined by faecal analysis. *Arnoldia (Rhodesia)* 5, 1-10.

Gusset, M. & Burgener, N. (2005). Estimating larger carnivore numbers from track counts and measurements. *African Journal of Ecology*, 43, 320-324.

Hamilton, P.H. (1976). *The movements of leopards in Tsavo National Park, Kenya, as determined by radio-tracking*. MSc thesis, University of Nairobi, Nairobi, Kenya.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *American Naturalist*, 94, 421-425.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T. & Wray, S. (1990). Home-range analyses using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, 20, 97-123.

Hart, J.A., Katembo, M. & Punga, K. (1996). Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *African Journal of Ecology*, 34, 364-379.

Hayward, M.W. (2009). Conservation management for the past, present and future. *Biodiversity Conservation*, 18, 765-775.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. (2006). Prey preferences of the leopard (Panthera pardus). *Journal of Zoology*, 270, 298-313.

Henke, S.E. & Bryant, F.C. (1999). Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management*, 63, 1066-1081.

Henschel, P. & Ray, R. (2003). *Leopards in African rainforests: survey and monitoring techniques*. Global Carnivore Program, Wildlife Conservation Society, available from: http://www.panthera.org/sites/default/files/LeopardManual_English_lowres.pdf (accessed 29/09/2010).

Henschel, P., Abernethy, K.A. & White, L.J.T. (2005). Leopard food habits in the Lopé National Park, Gabon, Central Africa. *African Journal of Ecology*, 43, 21-28.

References

Hunter, M.D. & Price, P.W. (1992). Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in naturall communities. *Ecology*, 73, 724-732.

Jackson, R.M. (1996). *Home range, movements and habitat use of snow leopard (*Uncia uncia*) in Nepal.* PhD. thesis, University of London, London, U.K.

Jackson, R.M., Roe, J.D., Wangchuk, R. & Hunter, D.O. (2005). *Surveying snow leopard populations with emphasis on camera trapping: a handbook.* The Snow Leopard Conservancy, Sonoma, California, U.S.A.

Jacobs, J. (1974). Quantitative measurements of food selection. *Oecologia*, 14, 413-417.

Jenny, D. & Zuberbühler, K. (2005). Hunting behaviour in West African forest leopards. *African Journal of Ecology*, 43, 197-200.

Johnson, S.D. (1992). Plant-animal relationships. In: Cowling, R.M. (ed.) *The ecology of fynbos. Nutrients, fire and diversity*, pp. 175-205. Oxford University Press, Cape Town, S.A.

Karanth, K.U. (1995). Estimating tiger *(*Panthera tigris*)* populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71, 333-338.

Karanth, K.U. & Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79, 2852–2862.

Karanth, K.U. & Nichols, J.D. (2000). *Ecological status and conservation of tigers in India*. Final Technical Report to the Division of International Conservation, U.S. Fish & Wildlife Service, Washington, D.C. and Wildlife Conservation Society, Centre for Wildlife Studies, Bangalore, India.

Karanth, K.U. & Nichols, J.D. (2002). *Monitoring tigers and their prey: a manual for researchers, managers, and conservationists in tropical Asia*. Centre for Wildlife Studies, Bangalore, India.

Keogh, H.J. (1979). *An atlas of hair from southern African species with reference to its taxonomic and ecological significance*. DSc thesis, University of Pretoria, S.A.

Keogh, H.J. (1983). A photographic reference system of the microstructure of the hair of southern African bovids. *South African Journal of Wildlife Research*, 13, 89-132.

Keogh, H.J. (1985). A photographic reference system based on the cuticular scale patterns and groove of the hair of 44 species of southern African Cricetidae and Muridae. *South African Journal of Wildlife Research*, 15, 109-159.

Kenward, R.E., Marcstrom, V. & Karlbom, M. (1993). Post-nestling behaviour in goshawks, *Accipiter gentilis*. II. Sex differences in sociality and nest switching. *Animal Behaviour*, 46, 371-378.

Kenward, R., South, A. & Walls, S. (2002). *Ranges 6.* AnaTrack Ltd., Wareham, Dorset, U.K.

Khorozyan, I. & Malkhasyan, A. (2002). Ecology of the leopard *(*Panthera pardus*)* in Khosrov Reserve, Armenia: implications for conservation. *Scientific Reports of the Zoological Society "La Torbiera"* 6, 1-41.

Knopff, K.H., Knopff, A.D., Warren, M.B. & Boyce, M.S. (2009). Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *Journal of Wildlife Management*, 73, 586-597.

Kohn, M.H., York, E.C., Kamradt, D.A., Haught, G., Sauvajot, R.A. & Wayne, R.K. (1999). Estimating population size by genotyping faeces. *Proceedings of the Royal Society of London,* 266B, 657-663.

Kure, N. (2003). *Living with leopards*. Sunbird, Cape Town, S.A.

Le Roux, P.G. & Skinner, J.D. (1989). A note on the ecology of the leopard *(Panthera pardus* Linnaeus*)* in the Londolozi Game Reserve. *African Journal of Ecology*, 27, 167-171.

Macdonald, D.W., Ball, F.G. & Hough, N.G. (1980). The evaluation of home range size and configuration using radio tracking data. In: Amlaner, C.J. & Macdonald, D.W. (eds) *A handbook on biotelemetry and radio tracking*, pp. 405-424. Pergamon Press, Oxford, U.K.

Macdonald, I.A.W. (1989). *Man's role in changing the face of southern Africa.* In: Biotic Diversity in southern Africa. Concepts and Conservation. Huntley, B.J. (ed), Oxford University Press, Cape Town, S.A.

Maffei, L., Cuéllar, E. & Noss, A. (2004). One thousand jaguars *(*Panthera onca*)* in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of* Zoology, 262, 295-304.

Manly, B.F.G., McDonald, L.L., Thomas, D.L., McDonald, T.L., & Erickson, W.P. (2002). *Resource selection by animals: statistical design and analysis for field studies*. Kluwer, Dordrecht, Holland.

Marker, L.L. & Dickman, A.J. (2005). Factors affecting leopard (Panthera pardus) spatial ecology, with particular reference to Namibian farmlands. *South African Journal of Wildlife Research*, 35, 105-115.

Martin, R.B. & de Meulenaer, T. (1988). *Survey of the status of the leopard* Panthera pardus *in Sub-Saharan Africa*. Lausanne: Secretariat on the Convention of International Trade in Endangered Species of Wild Fauna and Flora.

Martins, N. (2006). *Conservation genetics of* Panthera pardus *in South Africa: phylogeography of mitochondrial lineages*. MSc thesis, University of Bergen, Norway.

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. (2010). Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology*, doi:10.1111/j.1469-7998.2010.00757.x.

McCafferty, D.J. (2007). The value of infrared thermography for research on mammals: previous applications and future directions. *Mammal Review*, 37, 207-223.

McCarthy, T.M. (2000). *Ecology and conservation of snow leopards, Gobi brown bears, and wild bactrian camels in Mongolia*. PhD thesis, University of Massachusetts, Amherst, U.S.A.

McCarthy, T.M., Fuller, T.K. & Munkhtsog, B. (2005). Movements and activities of snow leopards in southwestern Mongolia. *Biological Conservation*, 124, 527-537.

Miller *et al*. (2001). The importance of large carnivores to healthy ecosystems. *Endangered Species Update*, 18, 202-210.

Miththapala, S., Seidensticker, J., Phillips, L.G., Fernando, S.B.U. & Smallwood, J.A. (1989). Identification of individual leopards (Panthera pardus kotiya) using spot pattern variation. *Journal of Zoology*, 218, 527-536.

Mizutani, F. & Jewell, P.A. (1998). Home-range and movements of leopards (Panthera pardus) on a livestock ranch in Kenya. *Journal of* Zoology, 244, 269-286.

Moen, R., Pastor, J. & Cohen, Y. (1996). Interpreting behavior from activity counters in GPS collars on moose. *ALCES*, 32, 101-108.

Mohr, C.O. (1947). Table of equivalent populations of North American small

mammals. *American Midland Naturalist*, 37, 223-249.

Monroy-Vilchis, O., Rodríguez-Soto, C., Zarco-González, M. & Urios, V. (2009). Cougar and jaguar habitat use and activity patterns in central Mexico. *Animal Biology*, 59, 145-157.

Mucina, L. & Rutherford, M.C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria, S.A.

Muckenhirn, N. & Eisenberg, J.F. (1973). Home ranges and predation in the Ceylon leopard. In: Eaton, R.L. (ed.) *The World's Cats. Vol.1, Ecology and Conservation*, pp. 142-175. World Wildlife Safari, Winston, Oregon, U.S.A

Nichols, J.D. (1992). Capture-recapture models: using marked animals to study population dynamics. *Bioscience*, 42, 94-102.

Norton, P.M. (1986). Historical changes in the distribution of leopards in the Cape Province, South Africa. *Bontebok*, 5, 1-9.

Norton, P.M. (1990). How many leopards? A criticism of Martin and de Meulenaar's population estimates for Africa. *South African Journal of Science*, 86, 218-219.

Norton, P.M. & Henley, S.R. (1987). Home range and movements of male leopards in the Cedarberg Wilderness Area, Cape Province. *South African Journal of Wildlife Research*, 17, 41-48.

Norton, P.M. & Lawson, A.B. (1985). Radio tracking of leopards and caracals in the Stellenbosch area, Cape Province. *South African Journal of Wildlife Research*, 15, 17-24.

Norton, P.M., Lawson, A.B., Henley, S.R. & Avery, G. (1986). Prey of leopards in four mountainous areas of the south-western Cape Province. *South African Journal of Wildlife Research*, 16, 47-52.

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T. & Paquet, P.C. (1996). Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology*, 10, 949-963.

Nowell, K. & Jackson, P. (1996). *Wild cats: status survey and conservation action plan*. Burlington Press, Cambridge, U.K.

Odden, M. & Wegge, P. (2005). Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. *Wildlife Biology*, 11, 145-152.

Oliveira-Santos, L.G.R. & Fernandez, F.A.S. (2010). Pleistocene rewilding, Frankenstein ecosystems, and an alternative conservation agenda. *Conservation Biology*, 24, 4-5.

Ott, T., Kerley, G.I.H. & Boshoff, A.F. (2007). Preliminary observations on the diet of leopards *(*Panthera pardus*)* from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology,* 42, 31-37.

Paine, R.T. (1980). Food webs: linkage, interaction strength, and community infrastructure. *Journal of Applied Ecology*, 49, 667-685.

Palomares, F. & Caro, T.M. (1999). Interspecific killing among mammalian carnivores. *American Naturalist*, 153, 492-508.

Parsons, S., Smith, S.G.D., Martins, Q., Horsnell, W.G.C., Gouse, T.A., Streichera, E.M., Warrena, R.M., van Helden, P.D. & van Pittiusa, N.C.G. (2008). Pulmonary infection due to the dassie bacillus (*Mycobacterium tuberculosis* complex sp.) in a free-living dassie (rock hyrax - *Procavia capensis*) from South Africa. *Tuberculosis*, 88, 80-83.

Powell, R.A. (2000). Animal home ranges, territories, and home range estimators. In: Boitani, L. & Fuller, T. (eds) *Techniques in animal ecology: uses and misuses*, pp. 65-110. Columbia University Press, New York, U.S.A.

Rabinowitz, A.R. & Nottingham, B.G. (1986). Ecology and behaviour of the jaguar *(*Panthera onca*)* in Belize, Central America. *Journal of Zoology,* 210, 149-159.

Rautenbach, T. (2010). *Assessing the diet of the Cape leopard (*Panthera pardus*) in the Cederberg and Gamka Mountains, South Africa*. Master's Thesis, Nelson Mandela Metropolitan University, South Africa.

Ray, J.C. & Sunquist, M.E. (2001). Trophic relations in a community of African rainforest carnivores. *Oecologia* 127, 395-408.

Rexstad, E. & Burnham, K.P. (1991). *User's guide for interactive program CAPTURE*. Fort Collins, CO: Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University, U.S.A.

Ripple, W.J. & Beschta, R.L. (2004). Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience*, 54, 755-766.

Ripple, W.J. & Beschta, R.L. (2008). Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation*, 141, 1249-1256.

Roche, C. (2008). 'The fertile brain and inventive power of man': anthropogenic factors in the cessation of springbok treks and the disruption of the Karoo ecosystem, 1865-1908. *Africa*, 78, 157-188.

Rodgers, A.R., Carr, A.P., Beyer, H.L., Smith, L. & Kie, J.G. (2007). *HRT: Home Range Tools for ArcGIS*. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Salom-Pérez, R., Carrillo, E., Sáenz, J.C., & Mora, J.M. (2007). Critical condition of the jaguar *Panthera onca* population in Corcovado National Park, Costa Rica. *Oryx*, 41, 51-56.

Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H. & Pedersen, H.C. (2005). Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, 33, 914-925.

Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In: Gittleman, J.L. (ed.) *Carnivore behaviour, ecology and evolution*, vol. 1, pp. 164-182. Chapman and Hall, London, U.K.

Schaller, G.B. (1972). *The Serengeti lion*. University of Chicago Press, Chicago, U.S.A.

Schippers, J. *et al.* (2008). The status of the world's land and marine mammals: diversity, threat and knowledge. *Science*, 322, 225-230

Seidensticker, J. (1976). On the ecological separation between tigers and leopards. *Biotropica*, 8, 225-234.

Seidensticker, J. (2002). Tigers: top carnivores and controlling processes in Asian forests. In: Wikramanayake, E., Dinerstein, E., Loucks, C. J., Olson, D. M., Morrison, J., Lamoreux, J., McKnight, M. & Hedao, P. (eds) *Terrestrial ecoregions of the Indo-Pacific, A Conservation Assessment*, pp. 56-59. Island Press, Washington D.C., U.S.A.

Shortridge, G.C. (1934). *The mammals of South West Africa*. Heinemann, London, U.K.

Silveira, L., Jácomo, A.T.A. & Diniz-Filho, J.A.F. (2003). Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation*, 114, 351-355.

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gomez, H. & Ayala, G. (2004). The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, 38, 148-154.

Skead, C.J. (1980). *Historical mammal incidence in the Cape Province. Vol.1: The western and northern Cape*. Cape Department of Nature & Environmental Conservation, Cape Town, S.A.

Skinner, J.D. & Smithers, R.H.N. (1990). *The mammals of the southern African subregion*. University of Pretoria, Pretoria, S.A.

Smallwood, K.S. & Fitzhugh, E.L. (1995). A track count for estimating mountain lion *Felis concolor californica* population trend. *Biological Conservation*, 71, 251-259.

Soisalo, M.K. & Cavalcanti, S.M.C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, 129, 487-496.

Spalton, J.A., Musalam al Hikmani, H., Willis, D. & Salim Bait Said, A. (2006). Critically endangered Arabian leopards *Panthera pardus nimr* persist in the Jabal Samhan Nature Reserve, Oman. *Oryx*, 40, 287-294.

Stander, P.E. (1997). Field age determination of leopards by tooth wear. *African Journal of Ecology*, 35, 156-161.

Stander, P.E. & Haden, P.J. (1997). The ecology of asociality in Namibian leopards. *Journal of Zoology*, 242, 343-364.

Stander, P.E. (1998). Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology*, 35, 378-385.

Stein, A.B., Fuller, T.K. & Marker, L.L. (2008). Opportunistic use of camera traps to assess habitat-specific mammal and bird diversity in northcentral Namibia. *Biological Conservation*, 17, 3579-3587.

Steyn, P.D.V. (2007). *The socio-spatial organisation of leopards (*Panthera pardus*) in the northern Tuli Game Reserve, Botswana.* Magister Technologiae: Nature Conservation, Tshwane University of Technology, Tshwane, S.A.

Stuart, C.T. (1981). Notes on the mammalian carnivores of the Cape Province, South Africa. *Bontebok*, 1, 1-58.

Stuart, C.T. & Stuart, M.D. (1991). *Cederberg leopard monitoring project*. Unpubl. report, African Carnivore Survey, Niewoudtville, S.A.

Sunquist, M.E. & Sunquist, F.C. (2002). *Wild cats of the world*. University of Chicago Press, Chicago, U.S.A.

Swanepoel, L. (2008). *Ecology of leopards (*Panthera pardus*) on selected game ranches in the Waterberg, Limpopo*. MSc thesis, University of Pretoria, Pretoria, S.A.

Swihart, R.K. & Slade, N.A. (1985). Influence of sampling interval on estimates of home range size. *Journal of Wildlife Management*, 49, 1019-1025.

Terborgh, J., & Estes, J.A. (2010). Conclusion: our trophically degraded planet. *Trophic cascades: predators, prey and the changing dynamics of nature.* Island Press, Washington, U.S.A.

Terborgh, J., *et al.* (2001). Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923-1925.

Thomas, P., Balme, G., Hunter, L., & McCabe-Parodi, J. (2005). Using scent attractants to noninvasively collect hair samples from cheetahs, leopards and lions. *Animal Keeper's Forum*, 7, 342-384.

Treves, A. & Karanth, K.U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, 17, 1491-1499.

Treves, A. & Naughton-Treves, L. (1999). Risk and opportunity for humans coexisting with large carnivores. *Journal of Human Evolution*, 36, 275-282.

van Rooyen, G., Steyn, H. & de Villiers, R. (1999). *Cederberg, Clanwilliam & Biedouw Valley: South African wild flower guide 10*. Botanical Society of South Africa, Cape Town, S.A.

Wallace, R.B., Gomez, H., Ayala, G. & Espinoza, F. (2003). *Journal of Neotropical Mammals*, 10, 133-139.

Wang, S.W. & Macdondald, D.W. (2009). The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation*, 142, 606-613.

Weber, W. & Rabinowitz, A. (1996). A global perspective on large carnivore conservation. *Conservation Biology*, 10, 1046-1054.

Wilting, A., Fischer, F., Bakar, S.A. & Linsenmair, K.E. (2006). Clouded leopards, the secretive top-carnivore of South-East Asian rainforests: their distribution, status and conservation needs in Sabah, Malaysia. *BMC Ecology*, 6, 1-13.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and extinction of populations inside protected areas. *Science*, 280, 2126-2128.

Worton, B.J. (1987). A review of models of home range for animal movement. *Ecological Modelling*, 38, 277-298.

Zimmermann, B., Wabakken, P., Sand, H., Pedersen, H.C. & Liberg, O. (2007). Wolf movement patterns: a key to estimation of kill rate? *Journal of Wildlife Management*, 71, 1177-1182.

APPENDIX 1

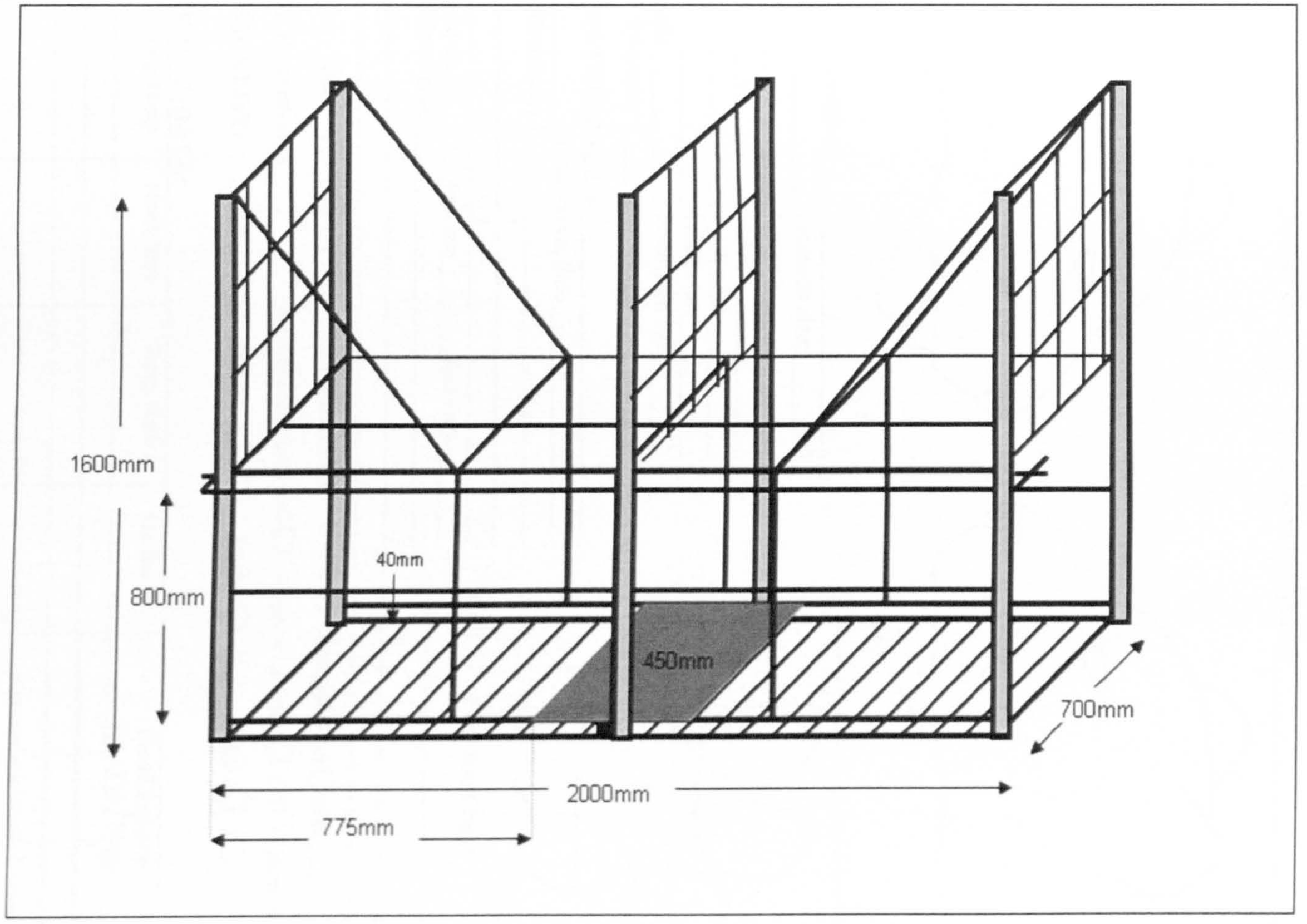


Figure 1: Three-door leopard cage trap.

APPENDIX 2

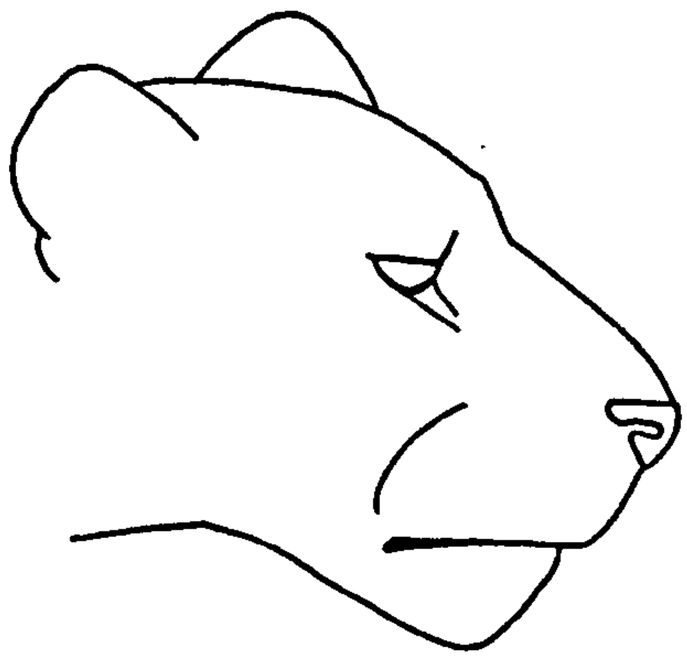
Provided by Dr Luke Hunter

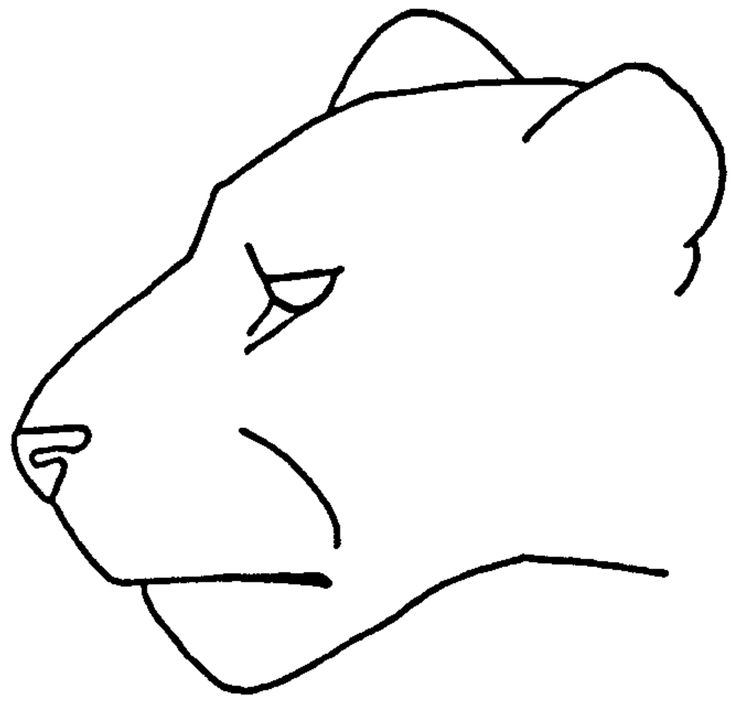
Recorder: _____

LEOPARD INDIVIDUAL RECORD.

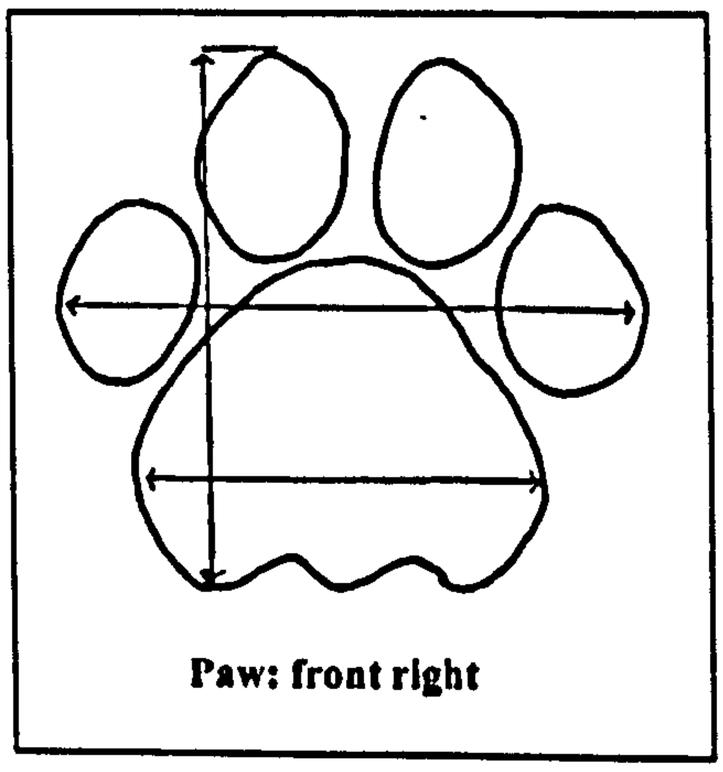
Unique ID_____Trovan # (Location)_____

Name_____Ranger ID_____Date/location captured_____





Sex _____Condition_____
Weight _____Stomach size:_____/ 5
Head-tail _____Curves:_____
Tail length _____Curves:_____
Chest girth _____Neck girth:_____
Head length _____Head circ:_____
Shoulder height _____Estimated age_____
Radio-collar frequency _____



Paw: front right

IMMOBILISATION Drug/dose_____
dart in, time_____animal down, time _____
top-ups (time/dose/route) 1._____
2,_____3_____
4_____5_____
Recovery: head-up_____first rise_____first walk_____
Recovery additional notes _____

SAMPLES: Tissue ☐ Hair ☐ Blood ☐ Faeces ☐ Tooth ☐ Ectoparasites☐desc_____

Haematology; time collected_____No Anticoagulant (red) ☐ Heparin (green) ☐ EDTA (purple) ☐

PHOTO CHECKLIST: Face r☐ l☐ Teeth r ☐ l☐ Body r☐ l☐ Tail r☐ l☐

PHYSIOLOGICAL DATA:

Time	Body Temp	Heart Rate	Resp. Rate	O2 Sat %	Blood Pressure Sys / Dia / Mean
					/ /
					/ /
					/ /
					/ /
					/ /

NOTES (females; include lactating, details of cubs, etc)_____

Notes for completing Leopard Individual Record sheets.

Recorder: person writing down the data.

Unique ID: animal's sex followed by sequential number e.g. Houdini is M1, April is F2 etc. The number is always unique and never repeated so each animal can be identified by the number alone. If the animal dies, the number is never re-used on a new animal.

Trovan: list number followed by the chip's location in parenthesis. Fit two chips, one beneath right ear and one in right flank.

Name: housename, optional.

Ranger ID: how animal is referred to by rangers (usually first line of whisker spots).

Date/location captured: location can be general or GPS/Grid ref.

Head profile diagrams: draw in whisker spots and any notches in the ears as well as facial scars. (Can also include cheek/eye spots which are unique to individuals though this is complicated and would be better recorded as a digital still). When transferring the data to electronic form, the digital stills of the face could be inserted here.

Measurements: see Diagram 1 which follows.

Head-tail. From nose tip to tail tip, not along curves (A-D on Diag 1): measure with tape alongside leopard laid out with straight neck and tail. Curves is the same measurement taken along curves with a flexible tape measure.

Tail Length. Tail tip to sacrum (B-C on Diag 1). Curves is the same measurement taken along curves with a flexible tape measure.

Chest girth. Measured around chest immediately behind forelegs ('armpits').

Neck girth. Measured immediately behind skull.

Head length. From back of skull (from end of sagittal crest which can be felt) to nose tip along curves.

Head circumference. Around cheeks with tape held against front edge of ears.

Shoulder height. From top of right scapula to front right foot as though in walking position (best taken from lower surface of plantar pad as though flat on ground); see Diag 1.

Paw measurements; refer to diagram. Each is the greatest distance between the two indicated points. Paw should be relaxed and not twisted for measurements. Also draw any distinguishing characteristics such as healed wounds (don't bother if superficial- they'll disappear).

Stomach Size: estimate how full, where 0 is starving and 5 is fully distended.

Estimated age; based on tooth wear: see attached Diagram 2.

Samples; check the box only for those taken during handling. Haematology- take blood in order indicated

Photographs: take photos (digital preferred) of each side of the animal's face, the teeth (each side), both sides of the body and both sides of the tail bands. Check off each in boxes provided.

Notes; include anything of interest and go over the page if required. For females include any details of pregnancy, lactation, if she has cubs (number/age/sex if possible) etc. Also include mention of any distinguishing characteristics beyond those recorded on head profiles.

Diagram 1: Guide for body measurements.
Dotted lines indicate approximate locations for skull, neck and chest measurements.

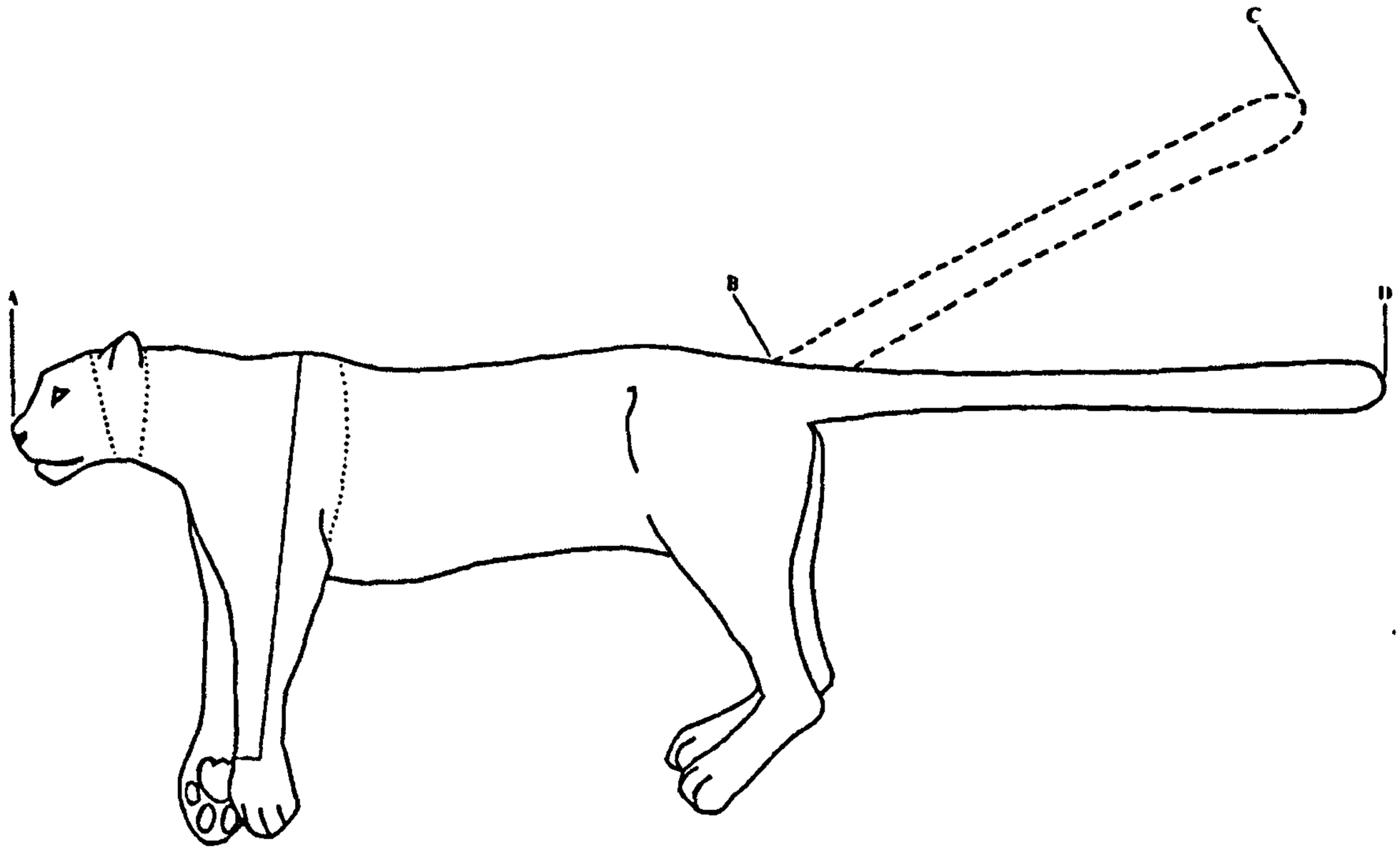
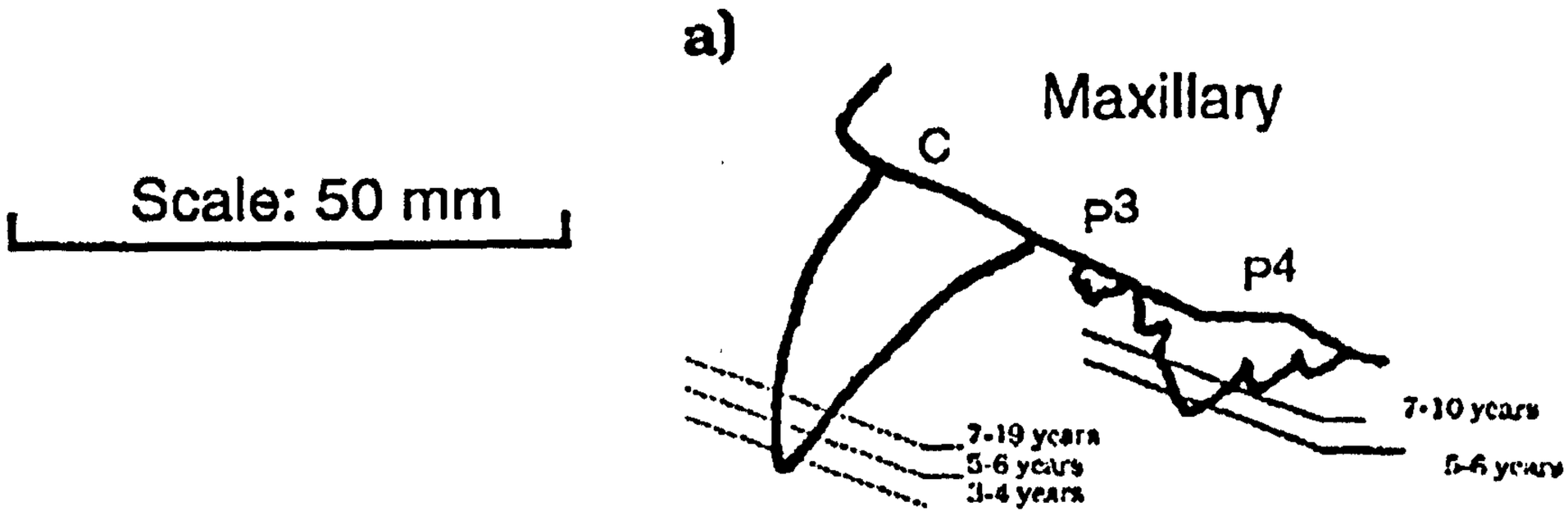


Diagram 2: Guide for aging leopards according to tooth wear (after Stander, 1997).



APPENDIX 3

Publications derived from this work

During the course of my studies I produced, facilitated or was involved in the following projects and publications:

1. Martins, Q. & Martins, N. (2006). Leopards of the Cape: conservation and conservation concerns. *International Journal of Environmental Studies*, 63, 579-585.
2. Martins, N. (2006). *Conservation genetics of* Panthera pardus *in South Africa: phylogeography of mitochondrial lineages.* MSc thesis, University of Bergen, Norway. The Cape Leopard Trust provided a scholarship for this study. I provided tissue samples for this study.
3. Parsons, S., Smith, S.G.D., Martins, Q., Horsnell, W.G.C., Gouse, T.A., Streichera, E.M., Warrena, R.M., van Helden, P.D. & van Pittiusa, N.C.G. (2008). Pulmonary infection due to the dassie bacillus (*Mycobacterium tuberculosis* complex sp.) in a free-living dassie (rock hyrax - *Procavia capensis*) from South Africa. *Tuberculosis*, 88, 80-83. I supervised American student Sarah Smith's University of Colorado biology internship involving dassie health.
4. Lindsay, P. (2008). *A spatio-temporal analysis of the habitat use of leopards (*Panthera pardus*) in the Karoo biome of the Cederberg Mountains, South Africa.* Honours Thesis, University of Cape Town, South Africa. I provided data as well as supervision of the student.
5. Rautenbach, T. (2010). *Assessing the diet of the Cape leopard (*Panthera pardus*) in the Cederberg and Gamka Mountains, South Africa.* Master's Thesis, Nelson Mandela Metropolitan University, South Africa. A scholarship was provided by the Cape Leopard Trust. I provided leopard scat samples and camera trapping data.
6. Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T., & Harris, S. (2010). Diet determination of the Cape mountain leopard using GPS location clusters and scat analysis. *Journal of Zoology*, doi:10.1111/j.1469-7998.2010.00757.x.

I have also initiated leopard population surveys in Namaqualand, Northern Cape, and the Gourtitz Corridor and Boland Mountains, both in the Western Cape. A PhD student has been given a full scholarship to conduct further ecological work on the spatial ecology of leopards in the Gouritz region of the Little Karoo.

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Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis

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Keywords
leopard; *Panthera pardus*; GPS; diet; location cluster analysis; depredation on livestock.

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Abstract

Studying leopards *Panthera pardus* in mountainous regions is challenging and there is little ecological information on their behaviour in these habitats. We used data from global positioning system (GPS) radio-collared leopards in conjunction with leopard scat analysis to identify key aspects of leopard feeding habits in the Cederberg Mountains of South Africa. We located 53 leopard kill/feeding sites from clustered GPS locations of ≥4 h and analysed 93 leopard scats. Both methods showed that klipspringers *Oreotragus oreotragus* and rock hyraxes *Procavia capensis* were the most common prey. GPS location clusters showed that the time leopards spent at a given location was positively related both to the probability of detecting prey remains and to prey size. Leopards made significantly more large kills in winter than summer ($P = 0.003$); there was no significant difference between male and female leopards in the average number of large kills or the average time spent at large kill sites. We show that, when studying large carnivores in inaccessible areas, it is important to use a combination of techniques to understand their feeding ecology and that GPS locations can be used to provide an accurate measure of diet even when small prey are being taken.

Introduction

Leopards *Panthera pardus* have the widest distribution of the large cats in Africa; yet their habits and feeding ecology outside savanna habitats are poorly understood (Norton *et al.*, 1986; Hart, Katembo & Punga, 1996; Henschel, Abernethy & White, 2005; Jenny & Zuberbühler, 2005). Throughout their range, they have a broad diet, feeding on mammals ranging in size from mice to eland *Taurotragus oryx* weighing up to 900 kg, as well as birds, reptiles and fish (Hamilton, 1976; Norton *et al.*, 1986; Bailey, 1993). Typically, leopards appear to take prey in proportion to their availability in a given area. In savannah, where medium- to large-sized ungulates predominate, most prey is in the 20–80 kg range (Hamilton, 1976; Bailey, 1993; Hayward *et al.*, 2006), whereas in African forested areas, where potential prey items are smaller, animals taken are in the 7–30 kg range (Hart *et al.*, 1996; Ray & Sunquist, 2001; Henschel *et al.*, 2005). Where larger animals are not available, leopards commonly feed on small prey <20 kg (Grobler & Wilson, 1972; Bothma & Le Riche, 1984; Norton *et al.*, 1986; Ray & Sunquist, 2001; Henschel *et al.*, 2005). In the mountains of the Western Cape, South Africa, where leopards are half the mass of leopards elsewhere in southern Africa (Stuart, 1981; Norton & Lawson, 1985), small prey such as rock hyrax *Procavia capensis* have been reported to form the majority of their diet (Norton *et al.*, 1986).

Leopard diet studies have typically used faecal analysis or direct observations in savanna or forest habitats (Grobler & Wilson, 1972; Bothma & Le Riche, 1984; Norton *et al.*, 1986; Le Roux & Skinner, 1989; Bailey, 1993; Bothma & Le Riche, 1994; Hart *et al.*, 1996; Henschel *et al.*, 2005). However, sightings of large predators such as leopards are rare in rugged and remote mountain areas and scats are hard to locate, making studies of their feeding habits difficult. VHF telemetry has been used to study leopard ecology, but with limited success (Norton & Lawson, 1985; Norton *et al.*, 1986; Bailey, 1993; Jackson, 1996). More recently, the use of global positioning system (GPS) radio collars has greatly enhanced our understanding of carnivore biology in remote areas through retrospective analysis of GPS location data (McCarthy, Fuller & Munkhtsog, 2005). Together with activity and home-range information, GPS collars have been used to locate and identify kills made by large carnivores such as wolves *Canis lupus* (Sand *et al.*, 2005; Demma, Barber-Meyer & Mech, 2007; Zimmermann *et al.*, 2007; Webb, Hebblewhite & Merrill, 2008) and cougars *Felis concolor* (Anderson & Lindzey, 2003; Knopff *et al.*, 2009) by investigating cluster locations (consecutive GPS fixes in close proximity to each other) over a period of several hours

or days. Generally, however, larger kills are located, and the value of GPS locations for identifying sites of smaller kills remains unclear (Knopff *et al.*, 2009).

Here, we use faecal analysis in conjunction with analysis of GPS cluster locations to study leopard feeding habits in the Cederberg Mountains, South Africa. Our aims were to (1) determine the diet of leopards in the Cederberg; (2) test whether leopard kill or feeding sites could be located using clusters of GPS locations and determine the significance of the time leopards spent at different feeding sites; (3) see whether there were seasonal differences in male and female feeding patterns; (4) compare GPS cluster location analysis with leopard faecal analysis to determine whether this was a reliable indicator of leopard diet in an area where they were believed to take small prey.

Methods

Study area

The study was carried out in the Cederberg Mountains, Western Cape, South Africa (32°27′S; 19°25′E; Fig. 1), *c.* 200 km north of Cape Town, an area with the highest leopard–farmer conflict in the Cape Province (Norton & Henley, 1987). Leopards here form part of a population extending continuously throughout the Cape folded mountains (Norton *et al.*, 1986). The Cederberg Conservancy, an area of 1710 km^2 in the Cederberg, was set aside by land owners as a leopard conservation area in 2007. Livestock farming with sheep, goats and cattle was the predominant land use until the 1990s. By 2005, livestock farming was reduced and wine production, olive and citrus farming in the valleys dominated in the area.

The 3000 km^2 study area was comprised equally of Fynbos and Succulent Karoo biomes (Mucina & Rutherford, 2006). Fynbos vegetation consisted of small shrubs, grass-like 'restios' interspersed with small trees (*Protea* species) and remnant populations of the endemic Clanwilliam cypress tree *Widdringtonia cedarbergensis*, whereas Karoo vegetation was dominated by small shrubs (<1 m high) and succulents (Mucina & Rutherford, 2006). The topography in both Fynbos and Karoo biomes consisted of rugged sandstone and shale mountains interspersed with open valleys and ravines (kloofs); the altitude varied from 200 to 2026 m. The climate of the area was subject to a relatively extreme seasonal temperature variation. During the study, temperatures ranged from −7 °C at night in winter to 47 °C on summer days (Q. Martins, unpubl. data). Annual rainfall varied from 200 mm (Karoo) to 1270 mm (Fynbos) (van Rooyen, Steyn & de Villiers, 1999). The austral summer extends from September to March and winter from April to August (Norton *et al.*, 1986). There was insufficient climatic variation to identify other seasons.

Most mammals in the study area were cryptic and/or nocturnal, and rarely observed. However, a camera-trapping study in the Karoo revealed 34 mammal species, including five small antelopes with a mass<25 kg (Q. Martins, unpubl. data). Of these, grey rhebuck *Pelea capreolus* was the largest, averaging 21 kg (Skinner & Smithers, 1990), and Cape grysbok *Raphicerus melanotis* was the smallest, averaging 10 kg. Our camera-trapping study showed that, of 773 small antelope photographic captures, 73% were klipspringer *Oreotragus oreotragus* (average mass 12.5 kg), 20% grysbok, 6% grey rhebok and <1% steenbok *Raphicerus campestris*. While camera data were not available for the Fynbos, sighting data suggest that klipspringer were most common. Some of the larger herbivores historically present, such as gemsbok *Oryx gazelle*, springbok *Antidorcas marsupialis* and Cape mountain zebra *Equus zebra*, had been reintroduced locally on private game reserves.

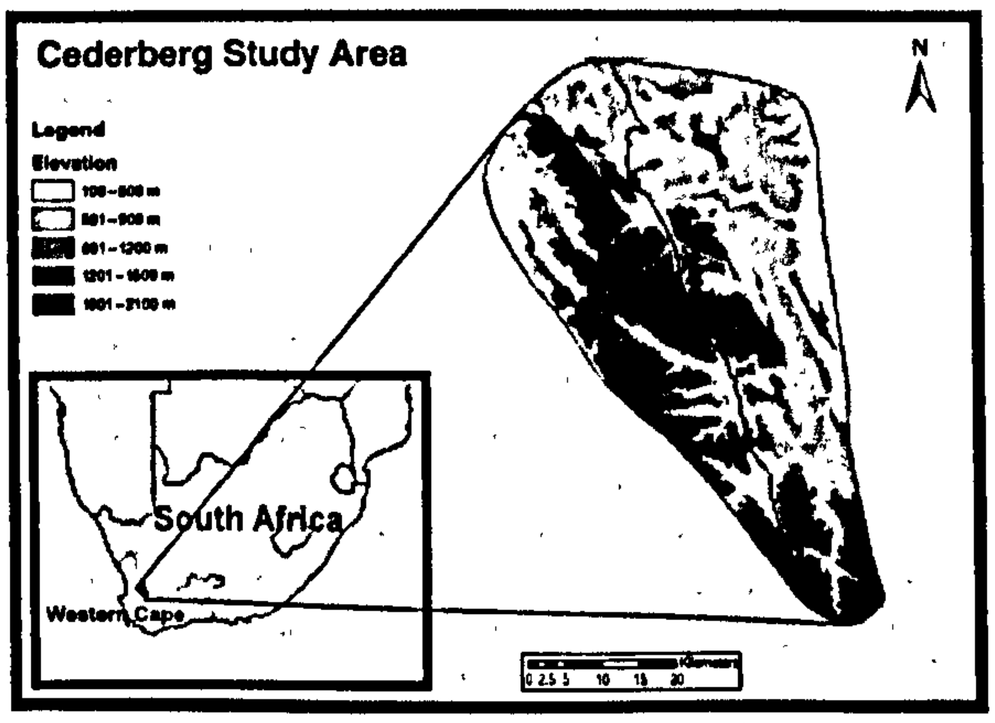

Figure 1 The Cederberg study area with key geographical features; Fynbos was to the west of the dividing line and Karoo to the east.

Leopard capture and immobilization

Leopards were trapped and radio-collared between 2005 and 2009 using double-door walk-through box traps measuring 2.0 × 0.80 × 0.75 m, placed on paths where leopards were expected or had previously been recorded during camera-trapping surveys. Cage traps were monitored twice a day: once visually and once using a VHF trap transmitter that signalled when the doors dropped. Leopards were anaesthetized by a veterinarian, initially using ketamine hydrochloride (Anaket-V, Bayer (Pty) Ltd., Isando, South Africa; dosage 10 mg/kg) mixed with xylazine hydrochloride (Chanazine, Bayer; (Pty) Ltd., Isando, South Africa; RSA; dosage 1 mg/kg) and subsequently with teletamine–zolazepam (Zoletil® 100, Virbac RSA (Pty) Ltd., Centurion, South Africa; dosage 5 mg/kg). Drugs were administered using a CO_2 dart pistol (DAN-INJECT ApS, Denmark). Sedated leopards were examined for general health and breeding condition, weighed, measured and aged by tooth colouration and wear (Stander, 1997). Collared leopards were placed in a holding cage and released once the effects of the anaesthetic had reduced sufficiently.

Capturing and collaring conformed to Western Cape Provincial Government's and American Society of Mammalogists' (Gannon, Sikes & the Animal Care and Use Committee of the American Society of Mammalogists,

2007) guidelines. Ethical approval was provided by CapeNature, the provincial nature conservation authority. Collars were removed on recapture of the animal.

GPS collars and location cluster analyses

VECTRONIC Aerospace GmbH (Berlin, Germany) GPS radio-collars, weighing <2% of an individual's body weight, were fitted to healthy adult animals. All collars had UHF remote GPS downloading capabilities and were programmed to capture and store 4–24 GPS locations per day. Collar schedules relied on collar performance. We attempted to obtain uninterrupted data for a full year. Because leopards in this region were predominantly nocturnal (Q. Martins, unpubl. data), collars were principally programmed to capture four to eight locations per day, with three to five of these being night-time locations (18:00–06:00) Central African Time. GPS data were downloaded by aircraft or on foot (from within 10 km) on a monthly basis where possible and plotted on 1:50 000 topographical maps using ArcView® 3.2. (ESRI, Redlands, CA, USA).

GPS clusters were investigated between August 2008 and April 2009. Clusters of locations that could signify potential feeding sites were defined as two locations within 50 m radius or >2 locations within 100 m of each other over a minimum 4-h period. We focused our attention on more recent kills (<1 year), but also investigated some older kills. Cluster analyses were conducted visually using the Arcview Moose-on-a-Leash function. Once potential feeding sites were identified, GPS coordinates were programmed into a handheld Garmin eTrex Venture® Cx (Garmin International, Olathe, KS, USA) and the central point in the tightest cluster was examined on foot. A maximum of 30 min was spent searching for prey remains within a radius of 50 m of this point. Bones, hair, horns, feet and hooves were collected and used to identify prey species. We calculated the biomass consumed from the average mass of the prey item.

Seasonal and sex differences in leopard diet

GPS location clusters provided the minimum time at a kill. We were unable to investigate all potential kills, but because sites occupied by a leopard for ≥24 h were indicative of them having made a kill >10 kg (see 'Results'), we analysed these potential kills made by individual leopards in both summer and winter over a 4-year period. Kill site analysis generated (1) the number of large kills; (2) the amount of time spent at these kills in both summer and winter. We compared seasonal and sexual differences using two-tailed Mann–Whitney tests. Where data were not available for an individual in one season, means were used. We used a generalized linear model with the binomial distribution with a single trial and the logistic link function to model whether a kill was found or not in relation to three explanatory variables: time from kill to time of investigation, time spent at the kill and season. We explored the allometric relationship between time on kill and the estimated mass of the prey by modelling the logarithm of time on kill in relation to the logarithm of prey mass.

Faecal analysis

Leopard scats were collected opportunistically between 2004 and 2008 in both Fynbos and Karoo habitats. As successive samples were collected infrequently over such a long period, we assumed that the same prey item was only represented in one individual scat. Scats were identified as belonging to leopards on one or more of the following criteria: (1) shape (Norton *et al.*, 1986); (2) scat diameter >20 mm (Norton *et al.*, 1986; Hart *et al.*, 1996; Khorozyan & Malkhasyan, 2002); (3) presence of leopard spoor or marking where the scat was collected; (4) the scat contained leopard hair ingested through interspecific killing or grooming (Ott, Kerley & Boshoff, 2007); scats <20 mm diameter were discarded unless leopard hair was present.

Dried scats were soaked in 4% formalin for 24 h, washed over a 1.5 mm sieve, the hair separated from other remains, and oven-dried at 60 °C (Norton *et al.*, 1986). Hair was cleaned in 96% alcohol and sulphuric ether mixture in equal measures (Keogh, 1979, 1983, 1985), washed in distilled water and left to dry.

Cuticular hair scale pattern was the main means to identify prey. Hair from each scat was evenly spread across a grid divided into forty-nine 25 cm^2 squares and an assortment of five hairs was selected from random blocks. Hair scale imprints made using nail varnish (Ott *et al.*, 2007) were compared with photographs from a reference collection at the Centre for African Conservation Ecology, Nelson Mandela Metropolitan University (Ott *et al.*, 2007, T. Rautenbach, unpubl. data), published photographs and keys and samples from animal skins. Macroscopic features, such as hair length and colour, aided identification, as did any remains of bone fragments, feet and hooves. We grouped individual species that were not identifiable; for example 'lagomorphs' included Smith's red rock rabbit *Pronolagus ruprestris*, Cape hare *Lepus capensis* and scrub hare *Lepus saxatilis*. Smaller rodents were also difficult to identify to the species level, although some were identified by teeth found in the scats (de Graaff, 1981). Birds and insects were classified to their order.

Results

Analysis of leopard diet using GPS location clusters

GPS data were collected from 10 adult leopards (seven males, three females) for periods ranging from 5 months (836 locations) to 18 months (3263 locations), mean ± SE (12 ± 1.2 months, 1781 ± 273.2 locations). The success rate at obtaining GPS locations was 75.8% (range 57.4–87.3%) of the total number of locations programmed for download.

Table 1 Leopard feeding remains located using clusters of GPS locations

	Number	Number of hours at kill site (range)	Weight range (kg)	Average weight (kg)	% of kills	% of total biomass
Lagomorph	1	4	0<10	1.6	1.9	0.2
Rock hyrax	16	4.0–24.0	0<10	3.8	30.2	6.6
Klipspringer	21	10.0–78.0	10<20	12.5	39.6	28.6
Grey duiker	4	24.0–48.0	10<20	19.7	7.6	8.6
Porcupine	5	10.0–28.0	10<20	17.5	9.4	9.5
Grey rhebuck	3	34.0–52.0	≥20	21.0	5.7	6.9
Livestock	2	66.0–92.0	≥20	70.0	3.8	15.2
Gemsbok	1	90	≥20	225.0	1.9	24.5

Livestock consisted of a goat and a calf; only one lagomorph, a Smith's red rock rabbit, was found. Weight ranges were divided into <10kg, 10<20 kg and ≥20 kg; average weights derived from Smithers (1990).

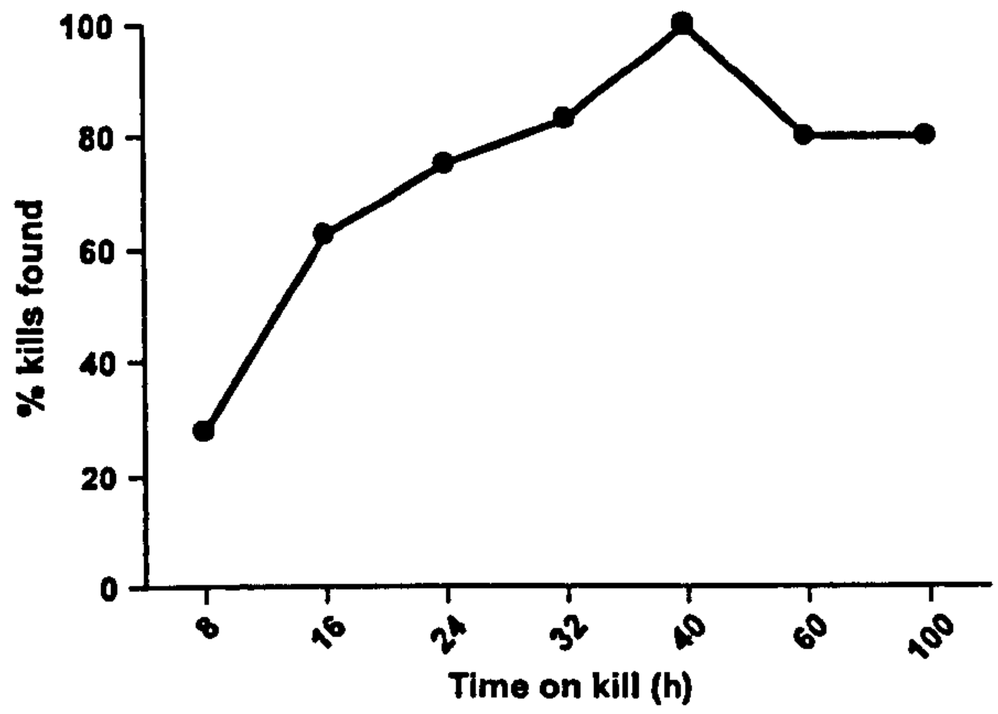

Figure 2 Proportion of kills found in relation to time a leopard spent in the vicinity of kill, based on global positioning system location clusters (n=101).

Of 101 GPS cluster locations identified and investigated as potential kill sites, we located 53 kills (52.5%). The majority of prey items consisted of klipspringers (39.6%) and rock hyraxes (30.2%) (Table 1). Other small antelope (grey duiker and grey rhebok) made up a further 13.3% of kills and porcupines *Hystrix africaeaustralis* 9.4%. Based on the average biomass, small antelope formed 44.1% of the diet, of which klipspringer was 28.6%, grey duiker 8.6% and grey rhebok 6.9%. Gemsbok (one) and livestock (goat and a calf) comprised 24.5 and 15.2% of the total biomass, respectively. One juvenile leopard killed and eaten by an adult male leopard was not included due to the difficulty in estimating time spent on the kill. Leopards consumed almost all of their prey for animals in the <25 kg class. Animal stomach contents were not eaten other than for small rodents, which leopards ate whole.

The successful location of animal remains correlated positively with the length of time the leopard had spent in the vicinity of the kill (Fig. 2). Successful location of a kill increased from 34.4% at sites occupied for <24 h to 83.8% for sites occupied for >24 h. Eighty-seven (86.1%) clusters investigated were <1-year old (Table 2). The generalized linear model to relate sex and time on kill to whether the kill was found showed that only time on kill was significant, viz.

Table 2 Percentage of GPS locations where a leopard *Panthora pardus* spent less or more than 24 h at which prey remains were found <1 year and >1 year later

Locations investigated	<1 year later	>1 year later	All
<24 h	34.4 (n=61)	33.3 (n=3)	34.4
>24 h	92.3 (n=26)	63.6 (n=11)	83.8
Total	51.7 (n=87)	57.1 (n=14)	52.5

$\text{logit}(P) = -1.027 + 0.0593t$, where P is the probability of finding the kill and t is time on the kill. The SE of the estimated regression coefficient for t was 0.0152 ($t = 3.90$, d.f. = 99, $P<0.001$). Backtransforming to probabilities, this suggests that the probability of finding the kill was 0.32 if $t = 6$ h, 0.39 if $t = 10$ h and 0.73 if $t = 34$ h. These three values were the lower quartile, median and upper quartile of observed time on kill. The allometric relationship between the estimated mass of prey m (kg) and the time on kill t (h) was $t = 3.05\,m^{0.828}$; the SE of the exponent was 0.0969 ($t = 8.55$, $r^2 = 0.59$, $P<0.001$). Thus, the mass of the prey accounted for 59% of time on the kill. The time interval between the kill and searching for it was not significant in predicting whether a kill was found regardless of how this variable was included in the set of explanatory variables.

Analysis of leopard scats

Scat analysis showed that klipspringer (44.1%) and rock hyrax (34.4%) were the most frequent prey items. Other species (Table 3) included aardwolf *Proteles cristatus*, small antelopes, lagomorphs, mongooses (three species) and porcupine. Smaller species (<2 kg), such as mongooses, rodents and birds, were not found using GPS location clusters but were identified in 19/93 (20.4%) leopard scats. However, they only accounted for <1% of prey biomass (13.1/1430.8 kg).

Species were present at comparable frequencies in both scats and at GPS-located kill sites for livestock (3.2 vs. 3.8%), rock hyrax (34.4 vs. 30.2%) and small antelopes grouped (51.5 vs. 52.9%). Of these, klipspringer remains were found in 44.1% of scats and at 39.6% of GPS-located kills (Fig. 3) ($\chi^2 = 3.70$, d.f. = 3, $P = 0.295$).

Table 3 Prey items recorded in leopard *Panthora pardus* scats in the Cederberg Mountains ($n = 93$)

Prey	Number of occurrences	Frequency of occurrence	% prey biomass
Klipspringer	41	44.1	35.8
Rock hyrax	32	34.4	8.5
Lagomorph	10	10.8	1.7
Small rodent	9	9.7	0.1
Grey rhebuck	7	7.5	10.3
Mongoose	6	6.5	0.6
Baboon	4	4.3	6.4
Bird	4	4.3	0.2
Cape grysbok	3	3.2	2.2
Goat	3	3.2	23.7
Grey duiker	3	3.2	4.1
Aardwolf	2	2.2	1.2
Porcupine	2	2.2	2.4
Springbuck	1	1.1	2.7
Total	127	136.6	100.0

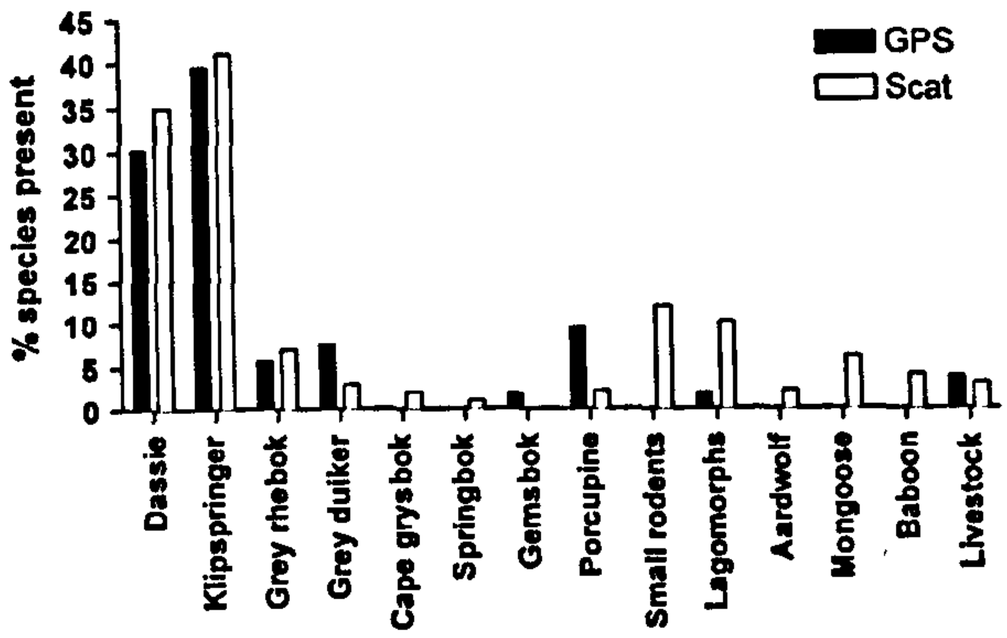

Figure 3 Comparison of species recorded in the diet of Cederberg leopards using scat analysis and global positioning system (GPS) cluster locations.

Predicting prey or prey mass from GPS location clusters

Animal remains recovered at potential kill sites revealed a positive correlation between the time spent in the vicinity of the kill and the estimated weight of the prey item (Fig. 4) ($r = 0.857$, $n = 53$, $P < 0.05$). Of kills when the leopard spent < 24 h in the vicinity, 72.7% represented prey species weighing < 3.8 kg ($n = 16$). When time spent on a kill was > 24 h, 96.7% ($n = 30$) were species weighing > 10 kg, usually ungulates or porcupines.

Seasonal variation in leopard diet using GPS clusters

In total, 107 months of GPS activity were analysed in both summer and winter, and 232 predicted larger kills of ≥ 24 h were detected, amounting to a minimum of 12 092 h at larger kills (mean 50.02 ± 18.05 h per kill). Using the average number of kills per season, leopards killed significantly more large prey in winter (mean 2.71 ± 0.50 per month; $n = 134$) than in summer (mean 1.77 ± 0.58 per month; $n = 98$) ($P = 0.003$). Shown as a function of time, this equates to an average of 148.0 ± 14.6 h month^{-1} in winter and 85.7 ± 19.0 h month^{-1} in summer ($P = 0.015$). However, for average number of large kills per month, there were no significant differences between male (2.35 ± 0.19) and female (2.01 ± 0.30) leopards ($P = 0.409$), nor for average time on large kills (131.2 ± 16.7 vs. 83.5 ± 18.8 h; $P = 0.174$).

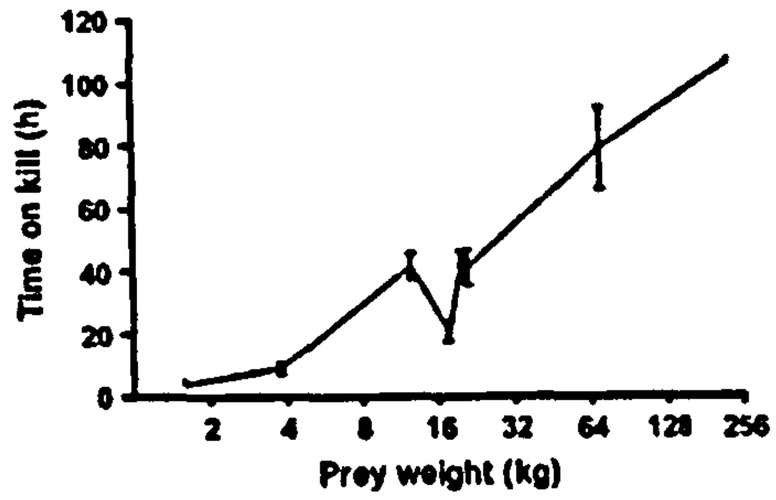

Figure 4 Mean number of hours (± SE) leopards *Panthora pardus* spent in the vicinity of a kill compared with prey weight range ($n = 53$, $r = 0.8571$, $P < 0.01$).

Discussion

GPS location cluster analysis has been used previously to study the diet of cougars in North America and wolves in Scandinavia (Anderson & Lindzey, 2003; Sand *et al.*, 2005; Zimmermann *et al.*, 2007); both kill rates and the probability of a kill taking place, based on number of nights a predator spent at a site, were investigated. These were predominantly the remains of large prey. Here, we have shown that GPS cluster locations can also be used to locate kills of a range of smaller prey items taken by a generalist predator and provide more detailed information on its feeding behaviour.

We recorded 23 species in the diet of leopards in the Cederberg Mountains; similar diversity has been recorded in other studies (Hart *et al.*, 1996; Ray & Sunquist, 2001; Henschel *et al.*, 2005) and is indicative of the generalist feeding behaviour of Cape leopards. However, in terms of biomass consumed, nine species (small rodents, birds and insects) represented < 1% of the total diet of leopards. Previous studies in the Cederberg reported the biomass of small ungulates and hyrax to be of equal importance in the diet (Norton *et al.*, 1986). We showed that small antelopes, in particular klipspringer, formed the greater part of the biomass consumed (scats = 57.7%; GPS = 44.1%) compared with rock hyrax (scats = 10.8%; GPS = 6.7%). Furthermore, whereas Norton *et al.* (1986) reported hyrax frequency in scats as 79.1%, we found this figure to be considerably lower (34.4%).

The prevalence of klipspringers and rock hyraxes in both scats and GPS data suggests a preference for leopards hunting in rugged, rocky terrain, the preferred habitat for

these prey (Skinner & Smithers, 1990). This differs from studies in other parts of the Cape mountains, where leopards mostly preyed on grysbok, which prefer denser vegetation along rivers or lower slopes (Norton *et al.*, 1986; Skinner & Smithers, 1990). Small prey such as rodents (excluding porcupine) and birds could not be located from GPS cluster analysis; however, their importance in terms of biomass consumed was negligible. One insect was recorded but was not considered part of their diet, as it was most likely feeding on the scat. Thus, scat and GPS techniques provided comparable results for identifying the most important prey of Cederberg leopards.

In rugged mountain areas where prey is small, predator kills are hard to locate without the assistance of GPS technology. In 5 years, we opportunistically encountered 18 confirmed leopard kills (eight rock hyraxes, six antelopes, three livestock and one porcupine) without the aid of GPS, but in 9 months, found 53 of 101 potential kills located by GPS cluster analysis. Kills were often hidden under bushes or rocky overhangs, unlikely to be found on an *ad hoc* basis, especially because leopards in the Cederberg Mountains consumed almost all of prey <25 kg. Remains would often only be part of a skull, hair and the rumen; because there were few scavengers in the area, kill remains could be located for up to 3.5 years. Finding kills using GPS clusters may not be as effective in areas where many scavengers are present or where floods also affect the chances of finding kills.

Our success rate at finding kills was a function of two measures of time; we were most successful at finding remains of kills <1-year old and where the leopard spent ≥ 24 h (92.3%). The success in locating a kill correlated positively to the length of time spent by the leopard at the kill site and prey mass. Kills where leopards fed on carcasses for ≥ 24 h consistently were prey weighing >10 kg. Large kills >40 kg were fed on for >66 h. The longest time spent at a location cluster was 184 h, which was probably a large domestic animal. Because there was a low probability of locating kills at sites occupied for <24 h, these could have included resting as well as kill sites. More intensive GPS schedules may assist in refining the technique for finding smaller kills, although this may be prohibitively labour intensive (Knopff *et al.*, 2009).

Analysing GPS clusters also enabled us to investigate potential differences between male and female leopard feeding behaviour. We found no significant differences between the number of larger kills made by males and females, although this could be due to the low sample size. Logging kills using GPS clusters ≥ 24 h also provided temporal data on leopard feeding ecology: leopards made more larger kills per month in winter than in summer. Historically, leopard depredation of livestock also occurred predominantly in winter (Stuart, 1981). GPS cluster analysis provides an important means of quantifying the impact of carnivore depredation on livestock. While remains of livestock eaten might be found from faecal analyses, any large animal fed on, such as a sheep or a cow, had a high probability of detection using GPS cluster analyses. Using this technique, we located kills of a goat (66 h) as well as a 10-month-old domestic calf (92 h). Kill sites occupied for >100 h were most likely cows, donkeys or, where present, large game. Thus, GPS cluster analysis can be used as an interactive means to find livestock kills and minimize conflict with livestock farmers by identifying high-risk areas and/or habitats.

This study demonstrated that the natural prey of leopards in the Cederberg Mountains consisted mainly of small- to medium-sized mammals weighing <20 kg, and that livestock and small prey such as rodents were an insignificant part of their diet. We found that feeding sites occupied for ≥ 24 h could be accurately detected by GPS analysis and that the time spent at prey sites correlated positively with the prey size. Thus, retrospective GPS analysis of predator movements in the Cederberg Mountains provided an accurate demonstration of leopard dietary habits and is a valuable tool for studying the feeding ecology of elusive carnivores that take a wide range of prey species and sizes.

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References

Anderson, C.R. & Lindzey, F.G. (2003). Estimating cougar predation rates from GPS location clusters. *J. Wildl. Mgmt.* **67**, 307–316.

Bailey, T.N. (1993). *The African leopard: ecology and behavior of a solitary felid.* New York: Columbia University Press.

Bothma, J.du P. & le Riche, E.A.N. (1984). Aspects of the ecology and the behaviour of the leopard *Panthera pardus* in the Kalahari desert. *Koedoe* **27** (Suppl.), 259–279.

Bothma, J.du P. & le Riche, E.A.N. (1994). Scat analysis and aspects of defecation in northern Cape leopards. *S. Afr. J. Wildl. Res.* **24**, 21–25.

Demma, D.J., Barber-Meyer, S.M. & Mech, L.D. (2007). Testing global positioning system telemetry to study wolf predation on deer fawns. *J. Wildl. Mgmt.* **71**, 2767–2775.

Gannon, W.L., Sikes, R.S. & the Animal Care and Use Committee of the American Society of Mammalogists. (2007). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **88**, 809–823.

de Graaff, G. (1981). *The rodents of southern Africa: notes on their identification, distribution, ecology and taxonomy.* Durban: Butterworth & Co.

Grobler, J.H. & Wilson, V.J. (1972). Food of the leopard *Panthera pardus* (Linn.) in the Rhodes Matopos National Park, Rhodesia, as determined by faecal analysis. *Arnoldia (Rhodesia)* **5**, 1–10.

Hamilton, P.H. (1976). *The movements of leopards in Tsavo National Park, Kenya, as determined by radio-tracking.* Unpubl. MSc thesis, University of Nairobi, Nairobi.

Hart, J.A., Katembo, M. & Punga, K. (1996). Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *Afr. J. Ecol.* **34**, 364–379.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. (2006). Prey preferences of the leopard (*Panthera pardus*). *J. Zool. (Lond.)* **270**, 298–313.

Henschel, P., Abernethy, K.A. & White, L.J.T. (2005). Leopard food habits in the Lopé National Park, Gabon, Central Africa. *Afr. J. Ecol.* **43**, 21–28.

Jackson, R.M. (1996). *Home range, movements and habitat use of snow leopard (Uncia uncia) in Nepal.* Unpubl. PhD thesis, University of London, London.

Jenny, D. & Zuberbühler, K. (2005). Hunting behaviour in West African forest leopards. *Afr. J. Ecol.* **43**, 197–200.

Keogh, H.J. (1979). An atlas of hair from southern African species with reference to its taxonomic and ecological significance. D.Sc. thesis, University of Pretoria, Pretoria.

Keogh, H.J. (1983). A photographic reference system of the microstructure of the hair of southern African bovids. *S. Afr. J. Wildl. Res.* **13**, 89–132.

Keogh, H.J. (1985). A photographic reference system based on the cuticular scale patterns and groove of the hair of 44 species of southern African Cricetidae and Muridae. *S. Afr. J. Wildl. Res.* **15**, 109–159.

Khorozyan, I. & Malkhasyan, A. (2002). Ecology of the leopard (*Panthera pardus)* in Khosrov Reserve, Armenia: implications for conservation. *Sci. Rep.Zool. Soc. "La Torbiera"* **6**, 1–41.

Knopff, K.H., Knopff, A.D., Warren, M.B. & Boyce, M.S. (2009). Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *J. Wildl. Mgmt.* **73**, 586–597.

Le Roux, P.G. & Skinner, J.D. (1989). A note on the ecology of the leopard (*Panthera pardus* Linnaeus) in the Londolozi Game Reserve. *Afr. J. Ecol.* **27**, 167–171.

McCarthy, T.M., Fuller, T.K. & Munkhtsog, B. (2005). Movements and activities of snow leopards in southwestern Mongolia. *Biol. Conserv.* **124**, 527–537.

Mucina, L. & Rutherford, M.C. (2006). *The vegetation of South Africa, Lesotho and Swaziland.* Pretoria: South African National Biodiversity Institute.

Norton, P.M. & Henley, S.R. (1987). Home range and movements of male leopards in the Cedarberg Wilderness Area, Cape Province. *S. Afr. J. Wildl. Res.* **17**, 41–48.

Norton, P.M. & Lawson, A.B. (1985). Radio tracking of leopards and caracals in the Stellenbosch area, Cape Province. *S. Afr. J. Wildl. Res.* **15**, 17–24.

Norton, P.M., Lawson, A.B., Henley, S.R. & Avery, G. (1986). Prey of leopards in four mountainous areas of the south-western Cape Province. *S. Afr. J. Wildl. Res.* **16**, 47–52.

Ott, T., Kerley, G.I.H. & Boshoff, A.F. (2007). Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *Afr. Zool.* **42**, 31–37.

Ray, J.C. & Sunquist, M.E. (2001). Trophic relations in a community of African rainforest carnivores. *Oecologia* **127**, 395–408.

van Rooyen, G., Steyn, H. & de Villiers, R. (1999). *Cederberg, clanwilliam & biedouw valley: south African wild flower guide 10.* Cape Town: Botanical Society of South Africa.

Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H. & Pedersen, H.C. (2005). Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildl. Soc. Bull.* **33**, 914–925.

Skinner, J.D. & Smithers, R.H.N. (1990). *The mammals of the southern African subregion.* Pretoria: University of Pretoria.

Stander, P.E. (1997). Field age determination of leopards by tooth wear. *Afr. J. Ecol.* **35**, 156–161.

Stuart, C.T. (1981). Notes on the mammalian carnivores of the Cape Province, South Africa. *Bontebok* **1**, 1–58.

Webb, N.F., Hebblewhite, M. & Merrill, E.H. (2008). Statistical methods for identifying wolf kill sites using global positioning system locations. *J. Wildl. Mgmt.* **72**, 798–807.

Zimmermann, B., Wabakken, P., Sand, H., Pedersen, H.C. & Liberg, O. (2007). Wolf movement patterns: a key to estimation of kill rate? *J. Wildl. Mgmt.* **71**, 1177–1182.